Liana Regeneration in Secondary and Primary Forests of Central Amazonia

Dissertation zur Erlangung des akademischen Doktorgrades
der Fakultät für Forstwissenschaften und Waldökologie
der Georg-August-Universität Göttingen

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Lianas are an important component of tropical forests. Despite their moderate contribution to forest biomass and diversity, they have a strong influence on forest dynamics. Lianas are particularly abundant in disturbed forest areas such as forest edges and small fragments, tree-fall gaps, and secondary forests. Because old growth forests are becoming more fragmented and the area covered by secondary forests is increasing, the importance of lianas is expected to increase. Studies of liana communities in forests mainly focus on stem densities of mature ascending plants. Data on liana seeds, seedlings, saplings and sprouts are scarce, but regeneration is implicated in ecological processes of all scales and may indicate future vegetation. Thus, knowledge about liana regeneration can be useful in forest management and conservation.

The objectives of the research were:

1) To assess how primary and secondary forests with different histories of land use are related to the density, diversity, traits and growth rates of liana regeneration,
2) To investigate the seed traits and germination characteristics of 20 liana species.

Field work was conducted in a primary forest and in two regionally dominant secondary forests in Amazonia near Manaus, Brazil. The primary forest was a non-inundated tropical evergreen lowland forest. The secondary forests were the *Vismia* forest, established after formerly clear cut land was used for pasture and intensively burned, and the *Cecropia* forest, established on formerly clear cut land but without pasture usage or intensive fires. Liana regeneration, which includes seedlings, saplings and sprouts ≤ 1.7m in length, was assessed in 8–10 plots per forest type, with a total of 27 plots used. The distance of the secondary forest plots to the next primary forest edges ranged between 0.03 and 1.2 km. Stand characteristics, such as canopy cover based on analyses of hemispherical photos, basal areas of trees and stem density of other growth forms, were investigated in each plot.

The first study investigated the density and species richness of liana regeneration in the three different forest types. The density of liana regeneration was 50% lower in the secondary forests than in the primary forests; whereas, the share of lianas on woody regeneration was similar in

all forest types. Species richness was highest in the primary forest and lowest in the *Vismia* forest. Accumulated species richness in the *Cecropia* forest was similar to that in the primary forest. With increasing distance from the primary forest, species richness and the proportion of lianas on woody regeneration in the secondary forests decreased; however, distance did not explain all variations between secondary forests. These results indicate that secondary forest types influenced species richness of liana regeneration but not liana density.

The second study focused on leaf and plant traits of the 26 most abundant species from the survey of the first part. Growth rate during one year and plant traits, that include specific leaf area, leaf size and shape, plant length, leaves per length, ratio of stem slenderness, and herbivory, were assessed at species and at community (plot) level. A principal component analysis suggested that most of the primary forest liana species exhibited similar plant and leaf traits and were characterized by short shoots and small, round leaves with low specific leaf area; whereas, secondary forest species had a broad range of trait characteristics. At the plot-level, separation of primary and secondary forest communities was confirmed. Plant size of lianas varied more within the secondary than within the primary forest plots. With increasing canopy cover, herbivory increased and variability of leaf size and plant length per plot decreased. The relative growth rate of lianas increased with decreasing canopy cover and was highest in *Vismia* forest plots. We concluded that plant functional characteristics of liana regeneration were more converged in the primary forest and differed substantially from secondary forests, yet canopy cover explained only partly the observed differences.

The third study presents seed and germination characteristics of 20 liana species. Biometrical data of seeds (mass, moisture content, longest and shortest axes, desiccation tolerance calculated by seed-coat-ratio) were collected and the seedling type was classified. Germination trials for desiccation tolerance and light dependence were conducted at constant 25 °C. For a subsample of species the influence of 12/12h alternating temperatures (20/30 °C and 15/35 °C, 12 h light) on germination was tested. Dry seed mass differed 1000 fold between species (0.009–10.7 g). Species with desiccation sensitive seeds all had above 0.27 g dry seed mass. In five species desiccation sensitive seeds were found where so far only desiccation tolerant seeds have been reported in the same genus or family. Light depending germination was found in three small seeded species (0.01–0.015 g) and was first described for two of these species; however, it has to be noted that the results are based on seeds of only one mother plant per species. Further studies should validate these findings. Alternating temperature influenced germination of four out of the nine species. Compared to constant temperature of 25 °C, daily

alternations between 15/35 °C always decreased the germination rate for these four species; alternations of 20/30 °C increased, decreased, or did not affect germination rate, depending on the species. The seed and germination characteristics of the studied species ranged from pioneer to climax traits, indicating that liana species could succeed in a range of environments.

In conclusion, the growth form liana comprised a range of leaf, plant and seed traits what emphazises the functional diversity of the group. The success of liana regeneration in disturbed habitats depends on species identity and environmental factors; thus, it is difficult to identify when, where and how lianas will benefit during forest succession.

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Lianenverjüngung in Primär- und Sekundärwäldern Zentralamazoniens

Lianen sind ein wichtiger Bestandteil tropischer Wälder. Obgleich sie nur im geringen Maße zur Waldbiomasse und -diversität beitragen, haben sie einen großen Einfluss auf die dynamischen Prozesse im Wald. Besonders in gestörten Waldflächen, wie Bestandeslücken, Waldrändern oder Sekundärwäldern, finden sich Lianen in hoher Abundanz. Da Primärwälder immer mehr fragmentiert werden und die Fläche der Sekundärwälder zunimmt, ist zu erwarten, dass die Bedeutung der Lianen in Zukunft steigt. Bisherige Untersuchungen zu Lianengesellschaften konzentrierten sich meist auf die Erhebung von Stammdichten großer kletternder Pflanzen. Dagegen gibt es wenige Informationen über Lianensamen, -keimlinge, -jungpflanzen und vegetative Sprosse (Trieb, Schössling), obwohl Verjüngung in viele ökologische Prozesse unterschiedlichster Skalen einbezogen ist und Hinweise auf die zukünftige Vegetation gibt. Das Wissen über die Verjüngung von Lianen kann für Naturschutz oder Waldbau von Bedeutung sein.

Die Ziele dieser Arbeit waren:

1) den Einfluss verschiedener Waldtypen wie Primärwald und Sekundärwälder mit unterschiedlicher Nutzungsgeschichte auf die Dichte, Artenvielfalt, funktionelle Pflanzenmerkmale und Wachstumsraten von Lianenverjüngung zu untersuchen,
2) die Samen- und Keimungsmerkmale von 20 Lianenarten zu bestimmen.

Die Freilanduntersuchungen wurden in einem Primärwald und zwei regional typischen Sekundärwaldtypen in Amazonien nahe Manaus (Brasilien) durchgeführt. Der Primärwald war tropischer immergrüner Tieflandregenwald. Die zwei Sekundärwaldtypen waren zum einen *Vismia*wald auf Flächen, die nach Kahlschlag abgebrannt und beweidet wurden, und zum anderen *Cecropia*wald auf ehemaligen Kahlschlagflächen ohne nachfolgende Beweidung oder intensives Abrennen. Lianenverjüngung, welche Keimlinge, Jungpflanzen und vegetative Sprosse $\leq$ 1,7 m Länge einschloss, wurde auf 8–10 Probeflächen pro Waldtyp erhoben, auf insgesamt 27 Probeflächen. Der Abstand der Sekundärwaldflächen zum Primärwald betrug zwischen 0,03 und 1,2 km. Bestandesmerkmale wie Kronendeckung, basierend auf hemisphärischen Fotos, Grundfläche des Baumbestandes und die Stammanzahl anderer Wuchsformen wurden auf allen Probeflächen aufgenommen.

In der ersten Studie wurden die Dichte und Artenvielfalt von Lianenverjüngung in den drei genannten Waldtypen untersucht. Im Sekundärwald war die Dichte der Lianenverjüngung 50 % geringer als im Primärwald. Der Anteil der Lianen an der Gesamtverjüngung aller holzigen Pflanzen unterschied sich allerdings nicht zwischen den Waldtypen. Die Artenanzahl pro Probefläche war im Primärwald am höchsten und am niedrigsten im *Vismia*wald. Die aufaddierte Artenanzahl war ähnlich im *Cecropia*- und Primärwald. Mit zunehmendem Abstand zum Primärwald nahmen der Anteil der Lianen an der Gesamtverjüngung sowie die Artenanzahl ab. Diese Ergebnisse zeigen, dass der Sekundärwaldtyp zwar die Artenvielfalt, nicht aber die Dichte der Lianenverjüngung beeinflusst.

Die zweite Untersuchung behandelte die funktionellen Pflanzen- und Blattmerkmale der 26 häufigsten Lianenarten aus der ersten Studie. Funktionelle Merkmale (spezifische Blattfläche, Blattgröße und -form, Pflanzenlänge, Schlankheitsgrad des Stamms und Herbivorie) sowie die Wachstumsrate während eines Jahres wurden pro Art und pro Probefläche evaluiert. Die meisten Primärwaldarten hatten eine ähnliche Form und waren durch kleinen Wuchs und kleine, runde Blätter mit geringer spezifischer Blattfläche gekennzeichnet, während die funktionellen Merkmale der Sekundärwaldarten stark variierten. Die Auswertung der funktionellen Merkmale pro Probefläche bestätigte den Unterschied zwischen Primär- und Sekundärwald. Mit zunehmender Kronendeckung nahm die Herbivorie zu und die Variabilität der Blattgröße ab. Die relative Wachstumsrate nahm mit steigender Kronendeckung ab und war am höchsten im *Vismia*wald. Aus den Ergebnissen kann man folgern, dass die funktionellen Merkmale der Lianenverjüngung im Primärwald ähnlich waren und sich deutlich von denen im Sekundärwald unterschieden; die Kronendeckung konnte jedoch nur einen Teil dieser Unterschiede erklären.

Der dritte Teil der Arbeit stellt die Samen- und Keimungseigenschaften von 20 Lianenarten vor. Biometrische Daten der Samen (Masse, Wassergehalt, längste und kürzeste Achse, die errechnete Austrockungstoleranz basierend auf dem Samen/Schalenverhältnis) wurden erhoben und der Keimlingstyp bestimmt. Zusätzlich wurden Keimversuche zur Untersuchung von Austrocknungstoleranz und Lichtabhängigkeit durchgeführt. Für einen Teil der Arten wurde der Einfluss von 12stündig wechselnden Temperaturen (20/30 °C, 15/35° C, mit 12 Lichtstunden) auf die Keimrate getestet. Die Trockenmasse der Samen unterschied sich 1000-fach zwischen den Arten (0,009 g–10,7 g). Die Arten mit austrocknungssensitiven Samen hatten alle Trockensamenmassen von ≥ 0,27 g. Für fünf Arten mit austrocknungssensitiven Samen wurde bisher in denselben Genera oder in einem Fall in derselben Familie nur von

austrocknungstoleranten Samen berichtet. Lichtabhängige Keimung wurde bei drei kleinsamigen Arten gefunden (0,01–0,015 g Samentrockenmasse) und für zwei dieser Arten erstmals beschrieben. Es muss jedoch berücksichtigt werden, dass nur Samen von einer Mutterpflanze pro Art untersucht wurden. Weitere Studien sollten die gefundenen Ergebnisse validieren. Wechselnde Temperatur beeinflusste die Keimung von vier von neun untersuchten Arten: Für alle vier Arten verminderte sich die Keimrate bei täglicher Temperaturschwankung zwischen 15 und 35 °C, bei wechselnde Temperaturen zwischen 20 und 30 °C war die Keimrate je nach Art vermindert, erhöht oder gleichbleibend im Vergleich zu konstanter Temperatur von 25 °C. Samen- und Keimungseigenschaften der untersuchten Arten reichten von typischen Pionier- bis zu Klimaxartenmerkmalen, was bedeutet, dass die Lianenarten in einer Bandbreite von Lebensräumen keimen könnten.

Diese Arbeit hat gezeigt, dass die Wuchsform Liane eine weite Bandbreite von Pflanzen- und Samenmerkmalen umfasst, womit die funktionelle Diversität dieser Gruppe unterstrichen wird. Der Erfolg der Lianenverjüngung in gestörten Habitaten ist artspezifisch und von verschiedenen Umweltfaktoren abhängig. Es ist somit schwer vorherzusagen, wann und wie Lianen während der Waldsukzession erfolgreich sind.

1. Introduction

1.1 Lianas

Lianas are one of the most conspicuous characteristics of tropical forests (Richards 1996). Even though they can be found in many climatic zones, they reach their highest abundance and diversity in tropical lowland forests (Gentry 1991a). Lianas are a taxonomically diverse growth form and are defined as woody climbers, which start growing from the ground, ascend to the canopy and stay rooted throughout their lives (Putz & Mooney 1991). Since they use other plants merely for support, they are so called structural parasites. Three major functional guilds depending on the modes of climbing can be distinguished: stem twiners, tendril twiners and branch twiners (Hegarty & Caballé 1991). Furthermore, other modifications for climbing exist, including roots, adhesive hairs or hooks (Fig 1.1). In a systematic view, lianas have developed independently in different taxa. Climbing gymnosperms exist (e.g. lianas of the genus *Gnetum*) as well as monocotyledonous lianas like the Asian climbing palm rattan (*Calamus* sp.) or *Smilax*. Many eudicot families ranging from the ancient Menispermaceae and Aristolochiaceae to more recent ones like Fabaceae and Bignoniaceae include climbing growth forms. A shared anatomical feature of lianas, or climbers in general, are the extremely long and wide vessels which ensure efficient water transport over long distances, but also make the plants susceptible for freezing damage (Ewers et al. 1991, Tyree & Ewers 1996). Even so a clear definition of lianas exists, transitional life forms such as climbing shrubs, subwoody persistent climbers and even woody hemiepiphytes may be included in liana surveys.

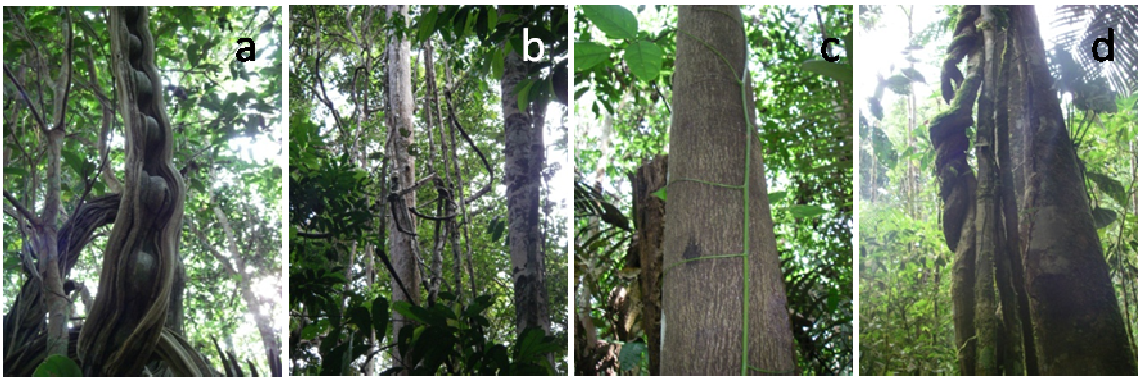

Figure 1.1: The stem form of liana ranges from ribbon-like (a) to round (d). Lianas connect trees (b) and use various modes of climbing e.g. stem winders (a, b, d) or using modified leaves (c). Often lianas climb upon the canopy using other lianas (d).

Lianas typically account for 25% of woody plant species in regions of tropical lowland forests, however, at site level this share might range from < 10% to > 40% (Gentry 1991, Appanah et al. 1992, Pérez-Salicrup et al. 2001, Schnitzer & Bongers 2002). They make up ~25% of woody stems (≥ 2.5 cm diameter) in tropical forests worldwide (Gentry 1991). Up to half of the trees, i.e. 34% to 50%, (≥ 10 cm diameter above breast height, DBH) in investigated neotropical and paleotropical forests had lianas in their crowns (Putz 1984, Putz & Chai 1987, Laurance et al. 2001). As structural parasites they invest little in structural support and allocate more resources in stem and root elongation, reproduction and leaf biomass (Putz & Mooney 1991). Due to this strategy, they usually contribute less than 5% of above-ground biomass of mature humid tropical forest, but can account for up to 30% of total foliage biomass and 40% of leaf litter fall (summarized by Hegarty & Caballé 1991). The diameter increment of lianas is very slow compared to trees which means that old growth forests can be identified by the presence of lianas with large diameter rather than by the presence of large trees (Emmons & Gentry 1983, Putz 1990, Schnitzer & Bongers 2002), (Fig. 1.2).

Figure 1.2: In old growth forest lianas can reach great diameters (a, b) and are especially abundant on tall trees with large diameters (c) (Putz 1984).

Lianas are an important component of forests and their influence on forest dynamics is severe, despite their delicate habit and small fraction of total biomass. They connect canopies and create an intercrown pathway for arboreal animals (Putz 1984, Emmons & Gentry 1983), offer habitats for many canopy insects (Odegaard 2000) and provide food that is especially important for primates (Emmons & Gentry 1983, Putz 1990). By linking trees together they also tear down neighbouring trees in cases of tree fall and are therefore a major concern for tropical silviculture. Lianas compete with trees for above- and below-ground resources (Schnitzer et al. 2005), and can suppress tree growth, decrease fecundity and encourage tree mortality (e.g. Putz 1984, Laurance et al. 2001, Schnitzer & Bongers 2002, Kainer et al. 2006, Heijden & Phillips 2009). They alter the competition among trees and therefore influence the dynamics and community of a forest. Some tree taxa are more likely to be infested than others, for example,

lianas suppress growth and inhibit abundance of slow growing, shade tolerant tree species but hardly affect pioneer species (Putz 1984, Schnitzer et al. 2000, Schnitzer & Carson 2001).

Lianas are known to reach especially high densities in naturally or anthropogenic disturbed areas, such as gaps or forest borders, (Laurance et al. 2001, Schnitzer & Bongers 2002) and are generally classified as a light demanding group (Putz 1984, DeWalt et al. 2000, Gerwing 2004). During forest succession liana stem density declines with increasing stand age and canopy closure (Putz 1984, DeWalt et al. 2000, Letcher & Chazdon 2009). In tree fall gaps lianas can dominate the regeneration so that vegetation is blocked in a low canopy state over many years (Schnitzer et al. 2000), they may also maintain their diversity by colonizing gaps (Schnitzer & Carson 2001). However, there are also records of numerous shade tolerant liana species (Putz 1984).

In Amazonia, like everywhere in the tropics, old-growth forests are becoming more and more fragmented and areas covered by secondary forests increase. Therefore, the importance of lianas in the remaining primary forest fragments and in forest regrowth is expected to increase in the future. Even in natural tropical forests, lianas have become more abundant in the recent past. Long term monitoring over the last two decades has detected increasing leaf biomass in central America (Wright et al. 2004a) and increasing density, basal area and size all over the neotropics (Phillips et al. 2002). The underlying process is not fully understood yet; probably lianas benefit from elevated CO_2 concentrations in the atmosphere (Granados & Körner 2002). Although lianas are very productive, they compensate only for a small fraction of biomass lost from death of trees so as a result less carbon gets fixed (Laurance et al. 2001).

For human use, various parts of diverse tropical climbers, e.g. fruits or fibre, are utilized. Of particular interest are the highly concentrated secondary compounds of many species for producing poisons or medicines, for example curare, alkaloids against plasmoids or vegetale insulin (Phillips 1991, Steele et al.1999, Pepato et al. 2003).

1.2 Regeneration

Regeneration of plants is the production of the next generation either by seeds or vegetative organs like resprouts of rhizomes or spreading by stolons (Black et al. 2006). The regeneration mode is determined by species specific features, e.g. dispersal characters or germination requirements, and its success is influenced by many biotic and abiotic factors including environmental microsite conditions, predation or herbivory. Plants have developed numerous strategies to secure success of regeneration, however five major functional types of regeneration can be distinguished (Grime 1979), of which four are applicable to woody plants: (a) vegetative expansion, (b) the formation of persistent seed banks, (c) the production of exceedingly wind dispersed seeds with limited persistence and (4) the establishment of seedling banks, where plants persist long term in a juvenile state.

Seeds, seedlings and sprouts are implicated in ecological processes of all scales – from the persistence or change of a single population to the diversity and dynamics of large units like communities, landscapes or local floras. Grime and Hillier (2000) postulated that the danger for ecosystem functions resulting from species loss, due to climate change or land use, is the impoverishment of seed rain and seedling banks. This leads to a decline of recruitment and subsequently often the traditional dominant vegetation is decreased and replaced by other species. Therefore, ecosystems lose their properties and convert into other land cover types. Knowledge of regeneration of species enables the prediction of the future vegetation coverage and is therefore important for silviculture or conservation management. For realistic predictions, changes of the environment during time e.g. light availability or competition during forest succession and microhabitat preference of seedlings and adults have to be considered, which can only be completed with prediction models. The base for any model is a databank that has to be filled with a minimum of information, which nowadays is readily available for grassland or tree species but is lacking for other growth forms such as lianas.

Knowledge about the regeneration of lianas is scarce. The number of publications about lianas has increased in the last few decades but most studies provide data on diversity, stem diameters or biomass of large sized lianas with stems $\geq$ 0.5 cm diameter (e.g. Laurance et al. 2001, Phillips et al. 2002). Compared to trees, lianas remain an understudied group and are usually excluded from forest inventories. Like other woody plants, lianas are able to regenerate by seeds, seedling bank or sprouting. Additionally, they also resprout immediately from fallen mature stems which normally survive the tree fall of their hosts (Putz 1984). Lianas can grow laterally into gaps and produce several independently rooted stems. Resprouts do not

necessarily compete with each other for above-ground resources since they are not restricted to vertical growth like trees, if enough support possibilities are provided. Studies on several species in the Neotropics showed that establishment and growth of liana seedlings required high light availability (e.g. Hättenschwiller 2002, Sanches and Válio 2002, Gerwing 2004, Dupuy and Chazdon 2006), however, there are also records of species specialized to median light levels (Gerwing 2004). On the other hand, juvenile lianas contribute a large proportion to the community of woody understory plants in mature forests which indicates shade tolerance at least during seedling or sapling stages (Richards 1996). Shade tolerance of regeneration has been shown in experiments and field surveys for several detailed studied liana species (Putz 1984, Hegarty & Caballé 1991, Gentry 1991b, Sanches & Válio 2002, Gerwing 2004). Disturbance, for example the removal of all seedlings from the forest floor, increased subsequent liana recruitment (Benítez-Malvido & Martínez-Ramos 2003); fire decreased the abundance of liana saplings more than that of trees (Kennard et al. 2002). Liana seed ecology is rarely studied because liana seeds are difficult to obtain and many liana species can reproduce asexually. However, reproduction by seeds is still important to secure genetic exchange, to increase the dispersal range and to overcome adverse conditions in the dormant stage. Seeds of liana species of the Amazon are predominantly wind dispersed (Gentry 1991b). The seeds of most liana species are suspected to be non-dormant (Baskin & Baskin 1998) and are probably desiccation tolerant.

1.3. Objectives

The general aim of the present study was to increase knowledge about regeneration of liana communities and to investigate when and if lianas benefit from disturbed environments during regeneration. This aim led to the specific objectives:

(1) to assess the influence of forest types with different land use histories, and the effect of the distance to primary forest on density and diversity of liana regeneration and compare these findings to primary forest.

(2) to assess the differences and variability of traits and growth of liana regeneration communities of different environments.

(3) to investigate seed traits and germination requirements that could predict germination success of a species in different environments, e.g. such as desiccation tolerance, light dependence, or tolerance to daily temperature alterations.

2. Methodology

2.1 Study site

The Amazon Basin, ranging over nine countries, is the largest continuous tropical rain forest in the world. The study site is located in the central Amazon (Fig. 2.1), 70–90 km north of Manaus, Brazil (2°20–25´S, 60°W) in the area of the Biological Dynamics of Forest Fragmentation Project, BDFFP (Lovejoy & Bierregaard 1990). Annual rainfall in Manaus averages 2285 mm (1961–1990, INMET 2010) with a distinct dry season from June to October. In the study area rain fall is assumed to exceed that of Manaus, and the dry season is presumed to be milder (Laurance 2001). The annual mean temperature is 26.7 °C (Lovejoy & Bierregaard 1990, Laurance 2001). The topography consists of plateaus and steep and deeply dissected valleys. Elevation ranges from 50–100 m above sea level (Laurance 2001). Soils were classified as nutrient poor acidic xanthic ferralsols (FAO 2003) with high clay content and the soil drains well (Ranzani 1980, Chauvel et al. 1987, Laurance et al. 1999).

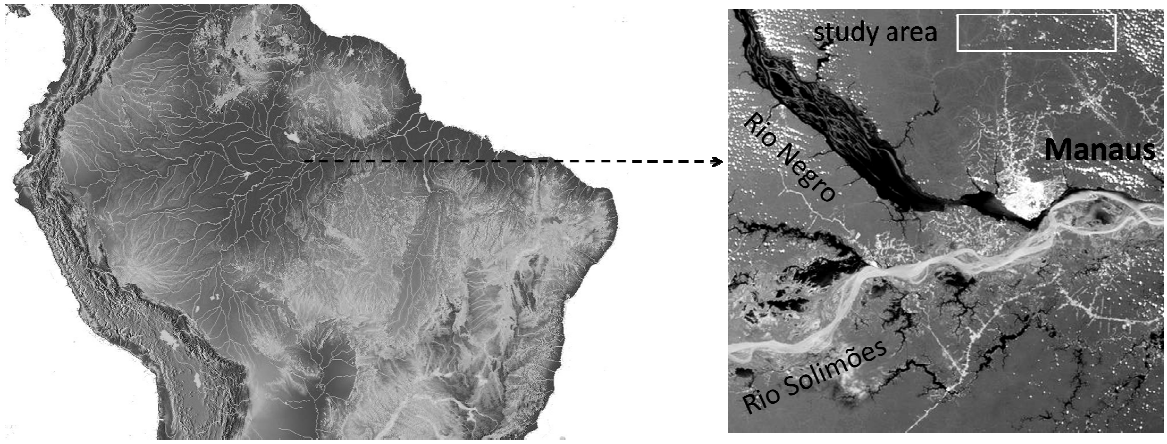

Figure 2.1: The Amazon Basin and greater area of Manaus including the study site. Map credits: maps-for-free.com and NASA (visibleearth.nasa.gov).

The mature vegetation is evergreen, non-inundated (terra firme) tropical lowland forest with trees 35–40 m tall and emerging trees that reach over 45 m (Rankin de Mérona et al. 1992). The density of trees is high (613 stems/ha, ≥10 cm diameter at breast height (DBH)), small trees are abundant, but few trees reach over 60 cm DBH (Laurance 2001). The understory is dense and has abundant stemless palms (*Astrocaryum* sp., *Attalea* sp.) (Lovejoy & Bierregrad 1990). The most abundant trees are from the families Lecythidaceae, Fabaceae, Sapotaceae and Burseracaeae, these families are also among the most species rich (Rankin de Mérona et al. 1992). Tree diversity in the greater area is among the highest in the world, with more than 1000

tree species (Rankin de Mérona et al. 1992, Ribeiro et al. 1999, Laurance 2001) and 280 tree species ha^{-1} ≥10 cm DBH (Oliveira and Mori 1999).

The project BDFFP was established in the 1980s. At this time the Brazilian government promoted cattle ranching in the Amazon and hence the clearing of forest land for pasture use (Lovejoy & Bierregaard 1990). 11 forest fragments of different sizes were isolated in three cattle ranches and 12 control areas of the same size were established in the neighbouring continuous forest. Today, in total eight research stations are used in three ranches and in continuous forest. Large parts of the former cleared areas are now covered with secondary forest. After forest clearance and before abandonment, some areas were actually used as cattle pasture for about four years and experienced repeated intense burnings (Mesquita et al. 2001). Secondary forest that established in these areas was, at the time of study (2007 to 2008), 17 to 19 years old (pers. comm. Vizcarra 2007). In this secondary forest type the tree community is dominated by the genus *Vismia* (Clusiaceae) and species of Melastomataceae (mainly *Belucia* sp.) and will be consequently referred as *Vismia* forest. Other areas had either hardly or not at all been burned after clear cut, mainly because the rainy season began very early in the year of clearance, and these areas have never been used as cattle pasture (Gascon & Bierregard 2001). Here, first a *Cecropia* (Urticaceae) dominated forest grew up (Mesquita et al. 2001) which was at the time of the study up to 25 years old. This forest type is characterized by a larger tree species diversity than the *Vismia* forest but usually has few or sometimes barely any *Cecropia* trees still alive. Nevertheless, in accordance with the former work of Mesquita et al. (2001) in this dissertation it will be referred as *Cecropia* forest. See Fig. 2.2.

Primary forest: high density of seedlings and understorey palms, tree stems of various sizes, high tree diversity

Cecropia forest: old (or dead) *Cecropia* sp. trees, diverse tree community, some stemless palms, high density of thin stemmed vines, thick litter layer of gross leaves.

Vismia forest: High density of thin stemmed trees of *Vismia* sp. or *Belucia* sp., sparse vegetation of grass (Poaceae) or *Selaginella* on the ground, less canopy closure.

Figure 2.2: Typical optical features of the three forest types used in the study of liana regeneration. Detailed structural data of forest stands are given in chapter 3, Table 3.1.

2.2. Sampling Design

27 plots were established in three forest types: 9 plots in primary forest, 10 in *Vismia* forest and 8 in *Cecropia* forest. One plot consisted of 3 long subplots (1.5 m x 30 m, Fig. 2.3) resulting in a total area of 135 m². The shape was chosen to assure access into the plots without stepping inside and to rediscover the single subplots easily. Within the subplots all lianas and other vegetation was surveyed. Trees ≥ 10 cm DBH were measured in addition to the subplots in the corridors in order to get a higher repetition number. Soil samples were taken in the corridors and hemispherical canopy pictures in the middle subplots. A 30 m x 30 m sampling area including the plot area was used for the survey of tall liana density (Fig 2.3).

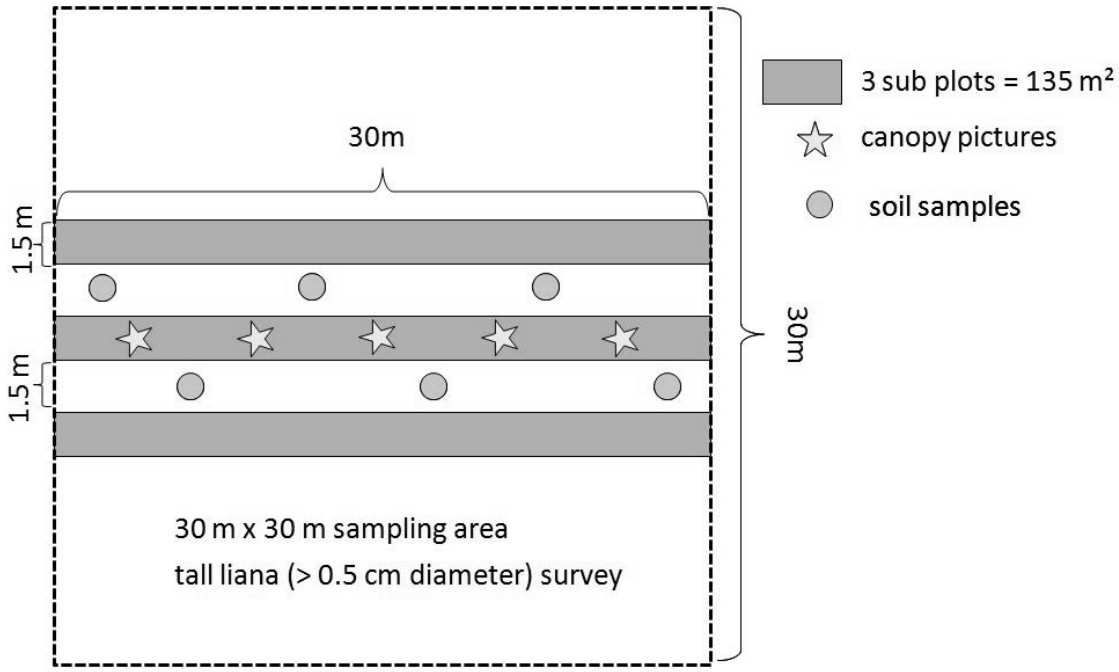

Figure 2.3: Plot design: In the grey subplots, lianas of all sizes were measured, in the 30 m x 30 m sampling area lianas ≥ 0.5 cm diameter were counted. Spots for canopy pictures and soil samples are indicated.

Due to given vegetation, the replicates per forest type within the research stations were not balanced (Fig. 2.4). As many plots as possible (14) were located next to plots of other, long-term projects (phytodemographic project and pioneer project, BDFFP), which provided well-distributed sites, easy access and additional information (*e.g.* tree height in the primary forest). If no permanent plots of these projects were available, plots were chosen to have a maximum distance to another plot of the same forest type, be on a plateau and be of about the same age and land use history in case of secondary forests. The plots of secondary forest were heterogeneous in terms of distance to primary forest edge and distance to pasture or trails. The

minimum and maximum distances to nearest primary forest edge were 25 m and 600 m respectively for plots in the *Cecropia* forest, and 45 m and 1200 m for plots in the *Vismia* forest.

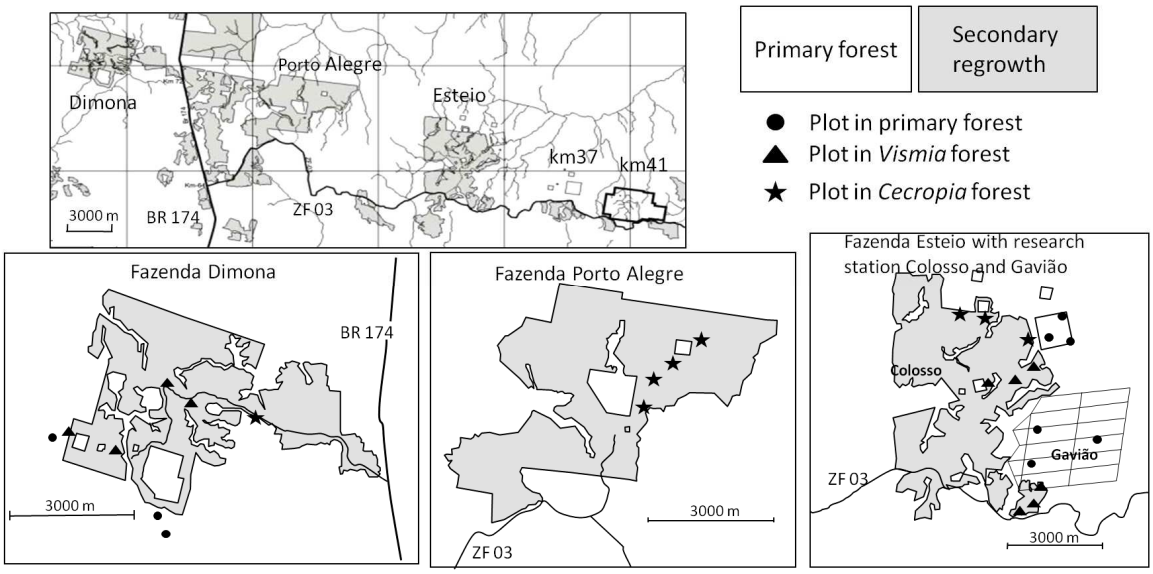

Figure 2.4: Distribution of the research stations and study plots in the area of the BDFFP. Source: BDFFP 1995 and redrawn after BDFFP.

2.3 Survey of lianas

Regeneration - From April to July 2007 all liana regeneration (seedlings, saplings and sprouts) up to 1.7 m in length were marked and length, number of leaves and length and width of the biggest leaf were measured. After twelve months (April to August 2008), all plants were surveyed again and also all overseen or new plants were included. Additionally, the diameters at the base (d_1), in the middle (d_2) and below the last leaf (d_3) were measured, the herbivory per leaf was estimated and the biggest, fully developed leaf was harvested for determination of specific leaf area. From the measured data several traits and the relative growth rate of height were calculated, details are given in Chapter 4. In cases of vegetative connection, only plants that were individually rooted entered the evaluation (Fig 2.5). In cases of several ground forking branches with one rooting point, the tallest was measured. It was noted if individuals were climbing or free-standing. Plants with skewed growth were regarded as support-needing, and therefore not free-standing when the maximum shoot length was at least twice the height above ground.

The origin of regeneration in the ground was detected by shallow digging and was assigned to three groups: (1) vegetative origin, like connection visible or sensible, or sprouts from old stumps/stems (2) seed or cotyledon visible or roots that originated from seeds, (3) not able to specify.

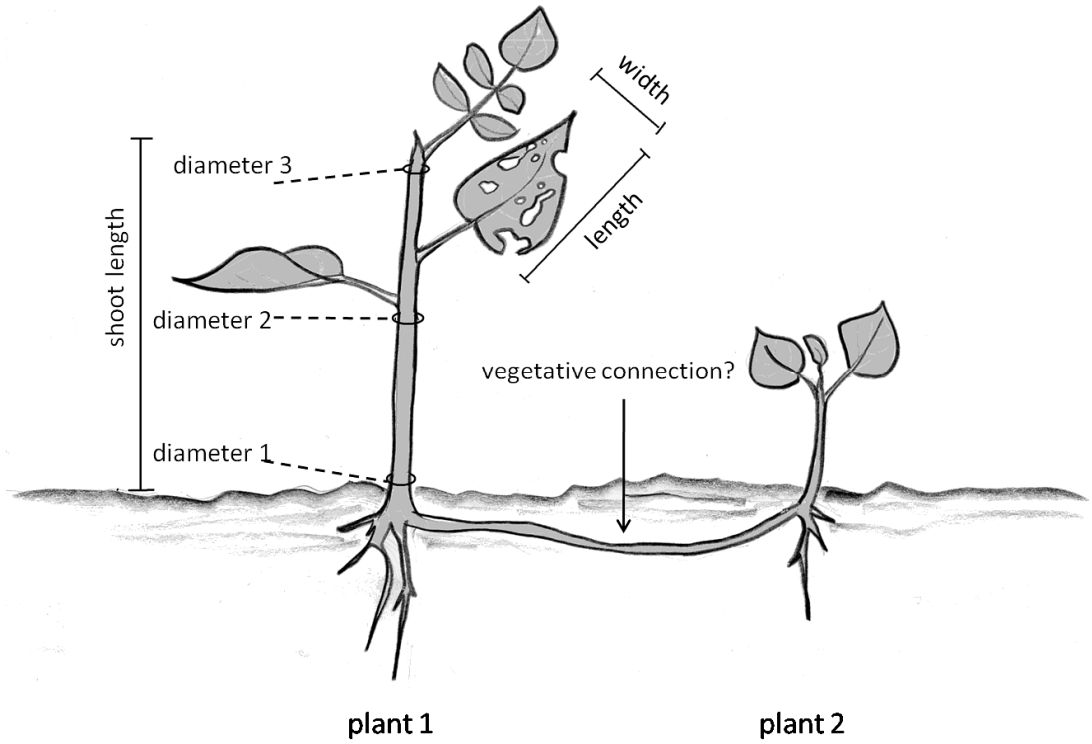

Figure 2.5: Example of individually rooted lianas that entered the evaluation as two plants, although vegetative connection existed. All conducted measurements are indicated at plant 1.

To verify the inclusion of all lianas in the study area, experienced parataxonomists inspected all plots. Plants were identified as morphospecies in the field and samples were taken as a voucher specimen outside the plots (in 2007) or the individual itself (in 2008), and sometimes additional photographs were taken at the site. Species identification was accomplished by comparison with specimens of the herbarium of the Instituto Nacional de Pesquisas da Amazônia (INPA) and with the help of parataxonomists. The species names follow the Flora da Reserva Ducke (Ribeiro et al. 1999) and the INPA herbarium. When identification at the species level was not possible, specimens were grouped as sp. A-Z within a genus or family. Absolute species numbers have to be considered with caution because of difficulties in identifying sterile small material and singletons. Specimens that could not be confirmed as liana were excluded from all data sets. Specimens were deposited at the INPA-Coordenação de Pesquisa em Silvicultura Tropical (CPST), Manaus. Species and morphospecies were separated into two growth habit groups based on literature or field

observations: (1) true woody species capable of reaching large diameters as well as the palm *Desmoncus polyacanthos* and *Smilax* sp., and (2) delicate lianas that seldom reach 1 or 2 cm diameter (e.g. *Sciadotenia eichleriana*) and vines with persistent but fibrous stems (*Mikania* sp., *Byttneria* sp., *Passiflora* sp.), henceforth termed 'fibrous lianas'. Hemi-epiphytes, epiphytes or climbing herbs were excluded. All growth forms included for analysis are consistent with the protocol on liana census by Gerwing et al. (2006).

Middle sized lianas - Lianas, that did not fulfil the criteria of regeneration nor of tall lianas (see next paragraph) were grouped together ('middle sized lianas', > 1.7 m height and < 0.5 cm diameter or > 1.7 m < 5 m height) and counted in the 135-m² plots. Separately rooted vegetative off sprouts were counted as separate stems. The diameter was taken following the same census as for tall lianas (see next paragraph) and where possible the height was recorded. Identification was not always possible, because access to leaves was difficult.

Tall lianas - Since the 30 m long plots served only for the evaluation of seedlings, a 30 m x 30 m sampling area was set up including the plot area (Fig 2.3). Within these 900 m² all lianas were measured and temporarily marked when they fulfilled following criteria: climbing (= not free standing), woody, reaching the canopy or in case of the primary forest, ascending the trees so high, that the end was not visible, ≥ 0.5 cm diameter at the measuring point. The measuring point was determined following Gerwing et al. (2006) and Schnitzer et al. (2008). In case of multiple stems each rooted stem ≥ 0.5 cm diameter was counted, however multiple stems of this size accounted only for 3 % of all stems. Diameter was measured with a manual calliper up to 5 cm, for stems exceeding 5 cm the perimeter was taken with a measuring tape. From elliptic or ribbon-like stems, two diameters were taken, the broadest (d_{broad}) and the thinnest side (d_{thinn}) and the diameter (d) was calculated as the geometric medium $d = \sqrt{d_{broad} \times d_{thinn}}$ (Gerwing et al. 2006). Calculated diameters smaller than 0.5 cm were excluded. Lianas in this group were not identified to species-level but could be clearly distinguished from trees, shrubs or hemiepiphytes.

2.4 Stand structural and soil data

All plants within the plots were counted and grouped into the life forms tree, palm, shrub and herb and into two size classes (≤ 1.70 m and > 1.70 m). For creeping vegetation, the percentage of cover was estimated. Diameter at breast height (DBH) was taken from trees ≥ 10 cm DBH.

For a more reliable estimation of stem density and basal area, the corridors were included, resulting in 225 m². In secondary forest plots, the height of ten trees and botanical families of all trees ≥5 cm DBH were noted.

Canopy coverage - In each plot five hemispherical photographs were taken with a digital camera (Nikon coolpix 4500) provided with a fish eye lens (Nikon FC E8 0.21x) and mounted on a tripod, levelled by a bubble level. The pictures were taken on the midline of the plot at a height of 0.73 m above the ground and a distance of 5 m from one point to the next in order to cover the whole plot area. The hemispherical pictures were analyzed for cover fraction of the canopy (f-cover) using the programme CAN_EYE V5 Hem (INRA, Avignon, France). The optical parameters were kept at default settings (optical centre row and line, horizon, radius), circle of interest was 60° and the sub sample factor was set at 2. The angular resolution was also kept at default (zenith 2.5°, azimuth 5°, zenith angle for the f-cover 0–10°).

Soil - In each plot, the thickness of the leaf litter layer was measured and the mineral soil (0–10 cm depth) was sampled at six locations in the corridors between the subplots. Two samples were combined into one mixed sample, resulting in three samples per plot. Samples were transported in micro perforated bags, air dried at approximately 35–40 °C for two weeks and afterwards sieved through a 2 mm mesh. Soil pH was measured in H_2O. Total nitrogen (N) was determined using Kjeldahl digestion, phosphorus (P) and potassium (K) were extracted with Mehlich I solution and determined with atomic absorption spectrophotometer (EMBRAPA 1999). Analyses were conducted in the laboratory of soil and plants (LTSP-INPA). Soil texture was determined by the “finger test” (VDLUFA Methodenbuch 1997).

2.5 Seeds

Mature seeds of 20 liana species from 12 families were collected close to their natural time of dispersal. Seeds (used here in a broader sense for diaspore) of most species were harvested from only one plant per species. Biometric data were obtained from at least 30 seeds (except two species with 15 and 25 seeds) and included fresh seed mass, moisture content, longest and shortest seed axes, and dry mass of seed coat (endocarp and/or testa) and of seed content (endosperm and/or embryo). Seed moisture content was calculated as the percentage of fresh mass. The ratio of seed coat to total seed mass was used to calculate the probability of desiccation tolerance or sensitivity *P* (DT/DS) based on Daws et al. (2006).

Germination trials were conducted at constant temperature of 25 °C with 12 h photoperiod or in complete darkness, and for species with sufficient seed material at 12/12 h alternating temperatures of 20/30 °C and 15/35 °C, where the period of higher temperature coincided with the 12 h light period. Desiccation tolerance was also tested in germination trials. Two sub-samples of seeds were dried in two steps (over ventilator and over silica gel) for approximately two weeks. Seed moisture was determined for a sub-sample, and the other seeds were re-hydrated slowly for seven days in an atmosphere with saturated relative humidity, avoiding eventual imbibition damage by direct contact with water (Ellis et al. 1990). Subsequently, seeds were sown at 25 °C and 12 h light (Fig. 2.6). Germination was assessed after radical protrusion (> 1 mm) and also after the development of a normal seedling (Bekendam & Grob 1979). Seedling type was determined according to the position and reserves of the cotyledons following the classification of Hladik & Miquel (1990) and Garwood (1996).

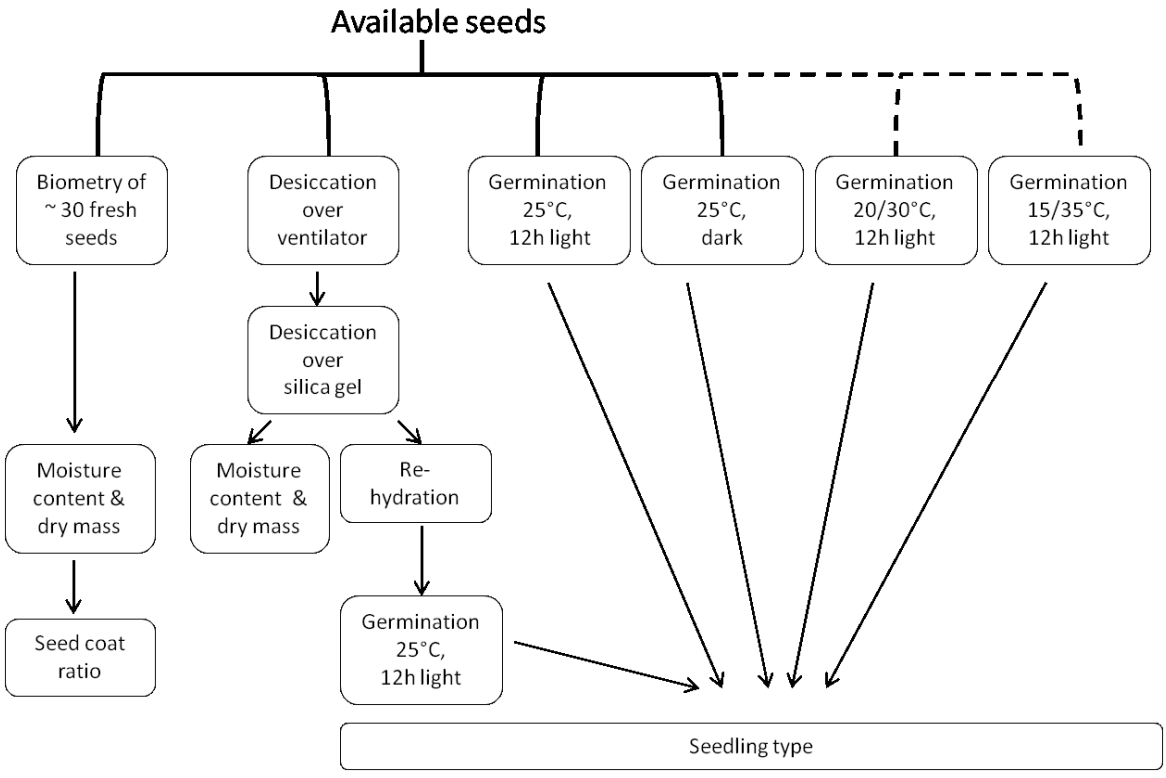

Figure 2.6: Schematic overview of the compartmentation of seeds for biometric measurements, desiccation treatment and germination tests. Total seed availability and repetition size for desiccation and germination test varied for the species. Treatments with dashed lines were only conducted for species of sufficient (> 300) seeds.

3. Liana Regeneration in Secondary and Primary Forests of Central Amazonia

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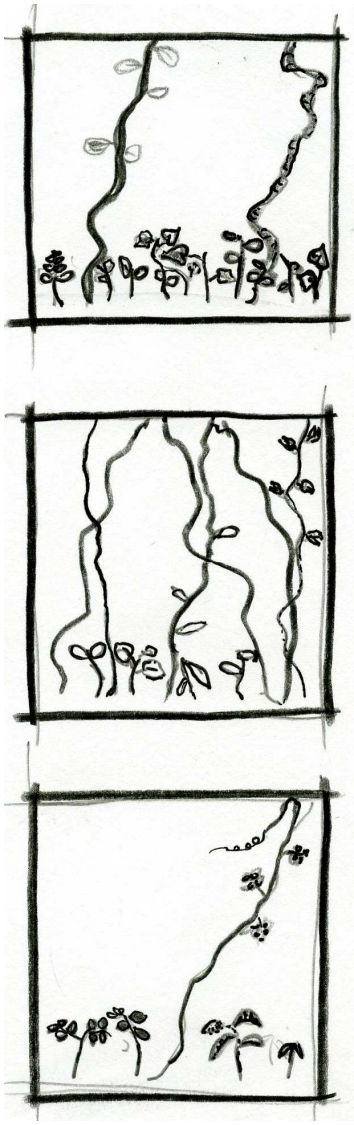

Abstract

Background: Lianas are considered to be particularly abundant in tropical forests after disturbance, however information on their regeneration by seedlings, saplings, and sprouts is scarce.

Aim: We assessed how forest types, primary vs. secondary forest types with different land use history are related to the density and diversity of liana regeneration.

Methods: Liana regeneration (≤ 1.7 m in length) was counted and identified in primary and secondary forest plots in Amazonia, near Manaus, Brazil. The primary forest was non-inundated evergreen tropical lowland forest. Secondary forest types were: *Vismia* (on land formerly clear cut, used for pasture and intensively burned) and *Cecropia* (on land formerly clear cut, no pasture usage nor intensive fires), with distances between 0.03 and 1.2 km to the primary forest edge.

Results: The density of woody regeneration (trees, lianas, palms and shrubs) was 50% lower in the secondary forests than in the primary forest. The share of lianas of woody regeneration (10-13%) hardly differed among forest types. Liana species richness per plot was highest in the primary forest and lowest in the *Vismia* forest. Accumulated species richness in the *Cecropia* forest was similar to that in the primary forest. With increasing distance from the primary forest, species richness and the proportion of lianas on woody regeneration decreased.

Conclusion: Our results indicate that secondary forest type/land use history influenced liana regeneration diversity but not density. Distance to primary forest influenced both.

Key words: density, diversity, seedlings, sprouts, terra firme, tropics

Introduction

Lianas are woody climbers that reach a maximum abundance in tropical lowland forests, where they significantly influence forest dynamics. These plants are frequent in old-growth or primary forests, and many studies have documented the increase in liana abundance following forest disturbance. In tree fall gaps, lianas can dominate regeneration for years (Schnitzer et al. 2000), and such gaps may play a central role in liana diversity (Schnitzer and Carson 2001). Moreover, the edges of forest fragments exhibit higher liana densities and diversities compared with undisturbed areas in the inner part of a continuous primary forest (Laurance et al. 2001). In secondary forests, recovering from a complete clearing of the original forest, lianas can be very common. For example, in the eastern Amazon, high liana abundances were recorded in successional forests on abandoned pastures (Uhl et al. 1988). In central Panama, 20 to 40 years old secondary forests exhibited higher liana abundance and diversity than old-growth forests (DeWalt et al. 2000). In Costa Rica, liana stem density was highest in secondary forests less than 20 years old, declined with increasing age of the secondary forest, and was lowest in the old-growth forest (Lechter and Chazdon 2009). On these sites, species richness of lianas showed no change or a slight decline with forest age, depending on the method of assessment (Lechter and Chazdon 2009). However, the cited studies considered only larger-sized lianas. The small-sized regeneration of lianas, important for consequent forest dynamics, has so far received little attention. According to Chazdon (2008), most studies of tropical forests including successional stages, have generally emphasised the tree component, while disregarding the dynamics of seedlings, saplings, and non-tree life forms.

Lianas reproduce by seeds or by sprouting, which enables them to colonise and become established in a broad range of habitats (Nabe-Nielsen and Hall 2002). They can survive falls from their host trees (Putz 1984) and afterwards can rapidly produce many ramets by sprouting from the stem on the ground. Although tropical lianas belong to various families, their seeds are primarily wind-dispersed and small (Gentry 1991b). Independent of the dispersal mode, the distance to seed source areas may influence liana regeneration density and diversity. The seedlings of several well-studied liana species in the Neotropics require high light availability for establishment and growth (e.g. Hättenschwiller 2002, Sanches and Válio 2002, Gerwing 2004, Dupuy and Chazdon 2006). On the other hand, the occurrence of many liana species under the closed canopy of primary forests point to shade tolerance during seedling or sapling stages, which has been shown by several detailed studies (Putz 1984, Hegarty and Caballé 1991, Gentry 1991b, Sanches and Válio 2002, Gerwing 2004). Intensive fires can decrease the abundance of liana

saplings more than that of trees, as indicated in studies from felling gaps in the tropical dry forest of Bolivia (Kennard et al. 2002). Based on earlier work, one may infer that several factors such as intensive fire, landscape position, and canopy cover affect liana regeneration. However, compared to other growth forms, studies on regeneration of liana communities, as opposed to studies on selected species are scarce, and these factors have yet to be addressed in a single study.

The objective of the present study was to assess the influence of forest types with different land use histories, and the effect of the distance to primary forest on the density and diversity of liana regeneration (< 1.7 m length). The study was conducted in a terra firme region of central Amazonia, where primary forests are very rich in tree species but liana density and diversity is considered medium (Gentry 1991a, Laurance et al. 2001). According to Mesquita et al. (2001), the two main types of secondary forest found in the region result from different land use histories. If clearcut land is used for cattle ranching and intensely burned, a secondary forest dominated by trees from the genus *Vismia* develops after land use is abandoned (Mesquita et al. 2001). If the primary forest is clear cut and not intensively burned, initially the genus *Cecropia* dominates, and afterwards a tree species assemblage develops that is more diverse than that in the *Vismia* forest (Mesquita et al. 2001).

Methods

Study site

The study was conducted in the area of the Biological Dynamics of Forest Fragments Project (BDFFP) (Lovejoy and Bierregaard 1990) located 70-90 km north of Manaus, Brazil (2°20-25´S, 60°W). The annual rainfall in Manaus averages 2285 mm (INMET 2010) with a June-October dry season. In the study area, the rainfall is assumed to exceed that of Manaus, and a milder dry season (> 150 mm per month) is presumed (Laurance 2001). The mean annual temperature is 26.7 °C in Manaus (Lovejoy and Bierregaard 1990). Soils were classified as nutrient-poor acidic xanthic ferralsols (Ranzani 1980, FAO 2003) with high clay content and well draining (Chauvel 1987, Laurance et al. 1999). Topography consists of plateaux and deeply dissected valleys. The elevation ranges from 50 to 100 m above sea level (Laurance 2001). Mature vegetation is evergreen, non-inundated (terra firme) lowland tropical forest with trees 35-40 m tall and emerging trees reaching over 45 m in height (Rankin de Mérona et al. 1992). Tree density is high, on average 613 stems per ha, ≥ 10 cm diameter at breast height (dbh). There are abundant small trees, but few large ones (> 60 cm DBH) (Laurance 2001). The most abundant trees species belong to the families of Lecythidaceae, Fabaceae, Sapotaceae and Burseracaeae (Gascon and

Bierregaard 2001). The tree diversity in the broader area is among the highest in the world, with over 1000 species (Rankin de Mérona et al. 1992, Ribeiro et al. 1999, Laurance 2001) and 280 species $ha^{-1} \geq 10$ cm DBH (de Oliveira and Mori 1999).

The BDFFP consists of forest fragments of different size that were isolated in the early 1980s, as well as control areas in the continuous forest. Several research stations are distributed in three cattle ranches (fazendas) and adjacent forests. Large parts of the formerly cleared area have since been covered with secondary forest. After initial forest clearance and prior to abandonment, for about 4 years, some of these areas were used as cattle pasture and experienced repeated intense fires (Mesquita et al. 2001). At the beginning of our study (2007), the secondary forest in these areas was 17 to 19 years old (T. Vizcarra 2007, pers. com.). As the tree community was dominated by the genus *Vismia* (Clusiaceae) and members of the Melastomataceae, forests on these former pasture lands will henceforth be referred to as *Vismia* forest. In areas that experienced few or no fires and no cattle ranching, *Cecropia*-dominated forest developed (Mesquita et al. 2001). This forest type of about 25 years old was characterised by greater tree species diversity than the *Vismia* forest. Although few living *Cecropia* (Urticaceae) trees remain, in accordance with the former work of Mesquita et al. (2001), we refer to this secondary forest as *Cecropia* forest.

Study design

Eighteen secondary forest plots (10 *Vismia* and eight *Cecropia)*, and nine primary forest plots were studied (Figure 3.1). As many plots as possible (14) were located next to plots of other, long-term projects (phytodemographic project and pioneer project, BDFFP), which provided well-distributed sites, easy access and additional information (e.g. tree height in the primary forest). The plots were all located on flat terrain and distributed on four research stations (Figure 3.1). A plot consisted of three long subplots (1.5 m x 30 m) with 1.5 m distance from each other. Total plot area was 135 m². A detrended component analysis (DCA) of log-transformed tree family data using tree stems ≥ 5 cm dbh confirmed the separation of the secondary forests into two groups. Eigenvalues were 0.48 for the first axis and 0.21 for the second. Together the two axes explained 35.4% of the total variance. Clusiaceae and Melastomataceae correlated with the first axis, R = 0.82 and R = 0.76, respectively.

For secondary forest plots, the distance to the nearest primary forest edge was estimated in the field and confirmed via Google Earth (Google Inc.). The minimum and maximum distances were 25 m and 600 m respectively for plots in the *Cecropia* forest, and 45 m and 1200 m for plots in

the *Vismia* forest. Stand structural characteristics of all three forest types are provided in Table 3.1.

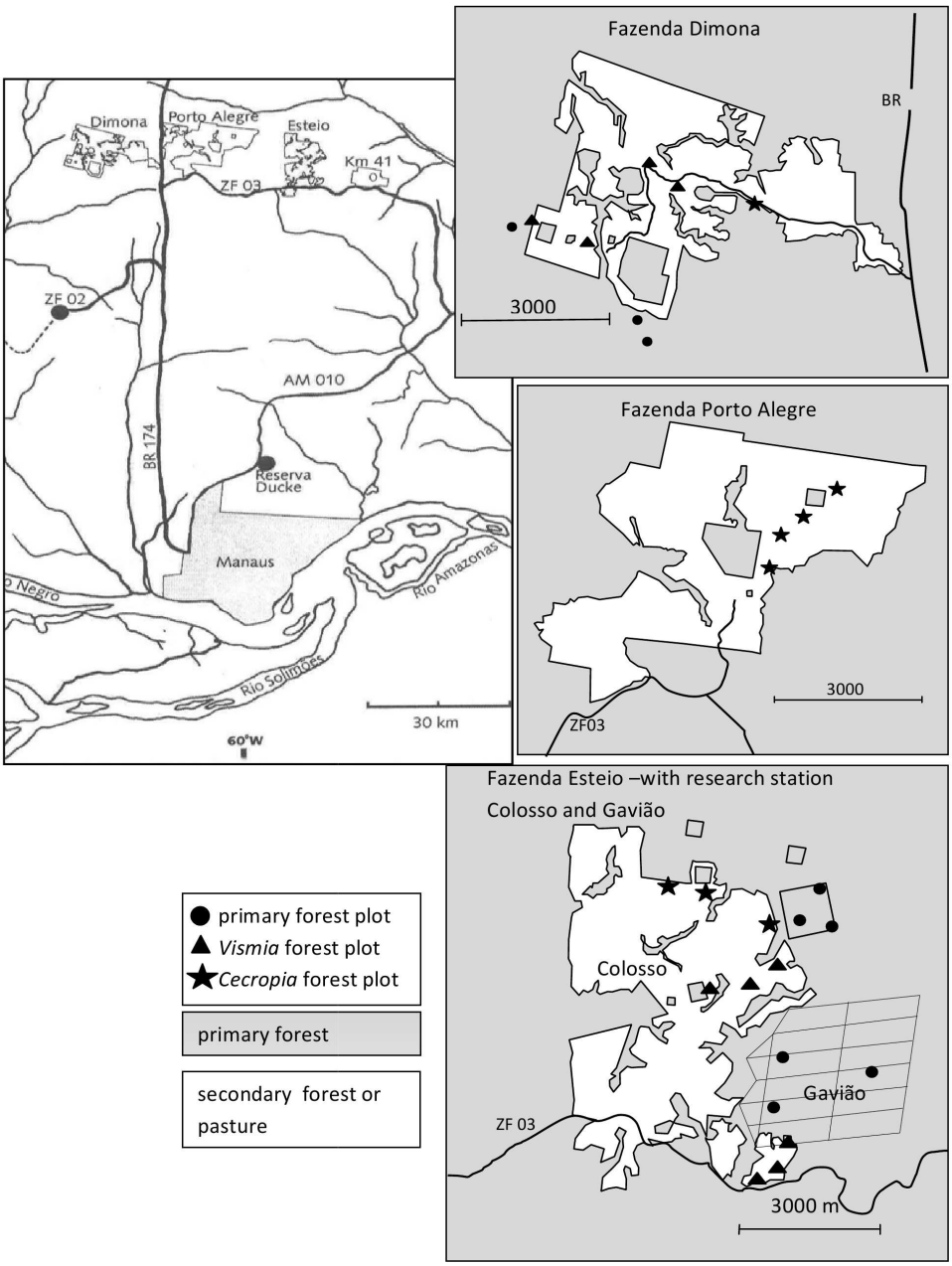

Figure 3.1. Location of the study site and plots. Source: BDFFP, 1990 & 1995.

Table 3.1. Forest structure and soil properties of our primary and secondary forest types near Manaus, central Amazonia. Values are means and standard deviations per site. Lowercase letters indicate significant differences ($P < 0.05$) in ANOVA followed by post-hoc Tukey HSD test. Tree height and distance to primary forest was compared with T-Test, †= literature data (Rankin de Mérona et al. 1992).

	primary forest	secondary forest	
		Cecropia	*Vismia*
number of plots	9	8	10
research stations	3	3	3
tree basal area (≥ 10 cm dbh, m²/ha)	33.2 ± 16.6 a	20.1 ± 5.7 b	16.5 ± 7.4 b
tree height (≥ 10 cm dbh, m)	35-40 (some 45)†	22.4 ± 2.8 a	17.7 ± 2.3 b
tree stem density (≥ 10 cm dbh n/ha)	721 ± 191 a	639 ± 184 a	756 ± 353 a
tree stem density (< 10 cm dbh n/ha)	6524 ± 1803 a	5417 ± 1917 a	6169± 3356 a
liana stem density (≥ 0.5 cm d., n/ha)	1025 ± 340 a	2147 ± 291 b	912 ± 594 a
cover fraction of canopy	0.87 ± 0.03 a	0.87 ± 0.05 a	0.74 ± 0.05 b
distance to primary forest (m)	-	176 ± 71 a	433 ± 143 a
thickness of litter layer (cm)	0.8 ± 0.7 a	1.6 ± 1.4 a	1.2 ± 1.0 a
mineral soil (0-10 cm)			
total N (g/kg)	1.4 ± 0.5 a	1.9 ± 0.6 a	1.7 ± 0.3 a
P (Mehlich extraction) (mg/kg)	3.5 ± 0.6 a	4.1 ± 1.2 a	3.1 ± 0.8 a
K (Mehlich extraction) (mg/kg)	22.4 ± 5.8 a	27.3 ± 6.4 a	25.1 ± 4.9 a
pH in H_2O (median)	4.1	3.9	4.1
soil texture	loamy sand	loam	clay loam

Liana regeneration

We marked and counted all liana regeneration (seedlings, saplings, sprouts) up to 1.7 m in length in all plots between April and August 2008. Plants were identified as morphospecies in the field and samples were taken as a voucher specimen outside the plots or the individual itself, and sometimes additional photographs were taken at the site. In case of vegetative connection, only plants that were individually rooted entered the evaluation. In case of several ground forking branches with one rooting point, the tallest was measured. It was noted if individuals were climbing or free-standing. In case of skewed growth, where the length was at least twice the height above ground, plants were regarded as support-needing, and therefore not free-standing. To verify the inclusion of all lianas in the study area, experienced parataxonomists inspected all plots.

Species identification was accomplished by comparison with specimens of the herbarium of the Instituto Nacional de Pesquisas da Amazônia (INPA) and with the help of parataxonomists. The species names follow the Flora da Reserva Ducke (Ribeiro et al. 1999) and the INPA herbarium. When identification at the species level was not possible, specimens were grouped as

sp. A-Z within a genus or family. Absolute species numbers have to be considered with caution because of difficulties in identifying sterile small material and singletons. Specimens that could not be confirmed as liana were excluded from all data sets. Specimens were deposited at the INPA-Coordenação de Pesquisa em Silvicultura Tropical (CPST), Manaus. All growth forms included for analysis are consistent with the protocol on liana census by Gerwing et al. (2006). Species and morphospecies were separated into two growth habit groups based on literature or field observations: (1) true woody species capable of reaching large diameters as well as the palm *Desmoncus polyacanthos* and *Smilax* sp., and (2) delicate lianas that seldom reach 1 or 2 cm diameter (e.g. *Sciadotenia eichleriana*) and vines with persistent but fibrous stems (*Mikania* sp., *Byttneria* sp., *Passiflora* sp.), henceforth termed 'fibrous lianas'. Since species richness per plot also depends on abundance, Fisher' alpha was used to calculate diversity, which is a relatively density-independent index.

The origin of liana regeneration was assessed in the field and included shallow digging and classification into one of three groups: (1) vegetative origin with verifiable connection or sprouts from old stumps/stems, (2) generative origin with seeds or cotyledons visible or roots that originated from seeds, and (3) unclear.

In addition to the lianas, we also counted all non-climbing plants within the plots, assorted them to the life forms of trees, palms and shrubs and grouped them into two size classes ($\leq$ 1.7 m and $\geq$ 1.7 m in height).

Tall, ascending lianas

Stem density of tall ascending lianas ($\geq$ 0.5 cm diameter) was determined in 27 sampling areas of 30 m x 30 m (900 m²), that were set up around every plot and included the original plot area of 135 m². The measuring point was determined by following Gerwing et al. (2006) and Schnitzer et al. (2008). In the case of multiple stems, each stem with a $\geq$ 0.5 cm diameter was counted, but multiple stems of this size made up only 3% of all stems. From elliptic or ribbon-like stems, two diameters were taken, the broadest (d_{broad}) and the thinnest side (d_{thinn}), and the diameter was calculated as the geometric medium (Gerwing et al. 2006). Lianas were not identified to species-level but could be clearly distinguished from trees, shrubs or hemiepiphytes.

Lianas, that did not fulfil the criteria of regeneration nor of tall lianas were grouped together ('middle sized lianas', > 1.7 m in length and < 0.5 cm diameter or > 1.7 m < 5 m in length) and counted in the 135-m² plots.

Soil

For each plot, the thickness of leaf litter layer was measured. The mineral layer (0–10 cm depth) was sampled at six locations per plot, and two samples were combined into one mixed sample, resulting in three samples per plot. Soil pH was measured in H_2O. Total nitrogen (N) was determined after Kjeldahl, phosphorus (P) and potassium (K) were extracted with Mehlich I solution and determined with atomic absorption spectrophotometer (EMBRAPA 1999). Soil texture was determined by the 'finger test' (VDLUFA Methodenbuch 1997).

Canopy cover

In each plot, five hemispherical photographs were taken with a digital camera (Nikon coolpix 4500) equiped with a fish eye lens (Nikon FC E8 0.21x) and mounted on a tripod. The photographs were taken on the middle line of the plot at a distance of 5 m from one point to the other and at a height of 0.73 m above the ground, which was above the average height of liana regeneration (0.3 m). The hemispherical pictures were analysed for cover fraction of the canopy (f-cover) using the programme CAN_EYE V5 Hem (INRA, Avignon, France).

Statistical analysis

Differences among the forest types (*Vismia* secondary forest, C*ecropia* secondary forest, and primary forest) were analysed by a one-way ANOVA and subsequent Tukey HSD post hoc test, in which our plots served as replicates. Prior to the analysis, the distribution of values was checked for normality with the Shapiro-Wilk test, for homogeneity of variances, with the Bartlett and the Levene tests and graphically for normal distribution of residuals. Nearly all variables were log-transformed to meet the conditions of ANOVA, except some square root transformed variables (density of liana and palm regeneration) and non-transformed data (species richness, Fisher's alpha, percentage of vegetative and generative liana regeneration). The difference between research station locations (Figure 3.1) was tested for primary forest plots with an ANOVA. ANCOVA was used to integrate distance to primary forest and canopy cover in the analysis of secondary forest data. For correlation, Pearson's product-moment correlation was used. Significance level was set at $P < 0.05$ for all analyses. Most statistical analyses were carried out with R-2.8.1 (R Core Development Team 2009). For the detrended component analysis (DCA) and species area curve PCord 5.0 (mjm software, Gleneden Beach, OR, USA) was used. DCA

was performed with log-transformed data of tree stems per family. Species-area curves were constructed by random subsampling of the data.

Results

Density of lianas

Stem density of tall, ascending lianas (stems ≥ 0.5 cm diameter, in 30 m x 30 m sampling areas), extrapolated to 1 ha was highest in *Cecropia* secondary forest at 2147 ± 291 SD, and significantly lower in the *Vismia* secondary forest (912 ± 594 SD) and in the primary forest (1025 ± 340 SD) (Table 3.1). The difference was primarily due to the high density of stems of up to 3 cm in diameter, which represented 93% of all stems in the *Cecropia* forest. Liana stems with ≥ 5 cm diameter were most abundant in the primary forest with an average of 73 stems ha^{-1}. The biggest observed liana stem found on primary forest reached 23 cm in diameter. *Cecropia* forest had 29 liana stems ha^{-1} ≥ 5 cm diameter and *Vismia* forest on average 4 stems ha^{-1}.

The density of middle-sized lianas per 135-m^2 plot did not significantly differ between forest types, yet liana abundance was slightly higher in secondary forest (*Cecropia* forest 12 ± 6 SD per plot and *Vismia* forest 11 ± 6 SD) than in primary forests (7 ± 4 SD per plot). This size class was less abundant per plot than tall lianas or regeneration.

Overall, the density of woody regeneration (trees, palms, shrubs and lianas) was significantly higher in the primary forest than in the secondary forests. Liana regeneration was 2.8 and 3.1 times more abundant in the primary forest than in the *Cecropia* and *Vismia* forest, respectively (Table 3.2). The density of liana regeneration did not differ significantly between the two types of secondary forest (Table 3.2). The density of tall lianas per sampling area and liana regeneration per plot were not correlated (R = -0.084, P = 0.678). Tree regeneration density was 2.7 and 3.5 times higher in the primary forest than in the *Cecropia* or *Vismia* forests, respectively. The density of palm regeneration in the primary forest was 3.2 times higher than in the *Cecropia* forest and 6.9 times higher than in the *Vismia* forest. Shrubs, mainly Piperaceae, were particularly abundant in the *Vismia* forest, where on average 200 shrubs per plot were encountered. Significantly fewer shrubs were found in *Cecropia* forest (60 shrubs per plot) and in the primary forest (nine shrubs per plot). The proportion of lianas of the total woody regeneration per plot was similar in all forest types: 13% in primary forest, 12% *Cecropia* and 10% in *Vismia* forest. Fibrous climbers (e.g. *Passiflora* sp. or *Mikania* sp.) contributed on average 17% of liana regeneration in *Vismia* forests, 8% in *Cecropia* forest, and only 1% in primary forest. The differences were not statistically

significant (Table 3.2). Most liana regeneration (86%) stood free and did not climb or lie on the ground. The smallest climbing plant recorded was 6 cm long. Free-standing plants were up to 1.7 m tall, which defined the upper limit of height included in our study. Slightly more climbing lianas occurred in the *Vismia* forest (19%) than in the *Cecropia* (15%) or in the primary forest (12%). However the differences were small and not statistically significant.

Regeneration that originated from seeds made up 55% of the liana regeneration in the primary forest and significantly less in *Cecropia* forest (20%); the share in the *Vismia* forest was in between (45%). In absolute numbers, the primary forest had more generative regeneration than the secondary forests. The share of vegetative sprouts was significantly higher in *Cecropia* forest (63%) than in the primary forest (28%), and intermediate in the *Vismia* forest (44%). The absolute numbers of vegetative regeneration did not differ among forest types. The origin of regeneration could not be determined for 16–26% of saplings (Table 3.2).

Distance to primary forest used as a covariate for all tested variables only influenced the share of lianas in the woody regeneration (Table 3.3). The percentage of lianas in regeneration decreased with increasing distance ($R = -0.644$, $df = 17$, $P = 0.004$). Canopy cover had no effect on any variable in the ANCOVA of secondary forest data (Table 3.3).

No differences were found for liana regeneration density ($F=0.408$, $df=2$, $P=0.682$) or tall lianas density ($F = 0.142$, $df = 2$, $P = 0.871$) among research stations for primary forest plots.

Table 3.2. Liana and other woody regeneration in primary forest and two types of secondary forest (*Cecropia* and *Vismia*) in central Amazonia. Values are mean (±SD) per 135 m² plot, significant highest values are in bold font. Differences between forest types in the Tukey Post Hoc test (significance level $P < 0.05$) are indicated by different lowercase letters. Plot numbers $n = 9$, primary forest; $n = 8$, *Cecropia* forest; $n = 10$, *Vismia* forest.

					primary forest	secondary forest	
						Cecropia	*Vismia*
		unit per plot	$F_{2,24}$	P	mean ± SD	mean ± SD	mean ± SD
regeneration density	liana	N	13.19	0.001	**142 ± 64** a	51 ± 21 b	46 ± 27 b
	trees	N	25.45	<0.001	**870 ± 241** a	319 ± 145 b	243 ± 150 b
	palms	N	30.05	<0.001	**84 ± 24** a	27 ± 21 b	12 ± 12 b
	shrubs	N	20.34	<0.001	9 ± 8 a	60 ± 60 b	**200 ± 143** c
	share of fibrous lianas on liana regeneration	%	2.58	0.097	2 ± 1 a	8 ± 7 a	17 ± 20 a
	share of lianas on woody regeneration	%	0.98	0.391	13 ± 6 a	12 ± 5 a	10 ± 5 a
liana diversity	species richness	N	10.50	<0.001	**26 ± 5** a	19 ± 7 ab	13 ± 7 b
	Fisher`s Alpha		2.04	0.152	10 ± 2 a	13 ± 7 a	8 ± 6 a
liana origin	generative	%	5.65	0.010	**55 ± 22** a	20 ± 13 b	45 ± 27 ab
	vegetative	%	5.66	0.010	28 ± 24 a	**63 ± 14** b	44 ± 23 ab

Table 3.3. Differences in liana regeneration between two types of secondary forest in central Amazonia, as a function of distance to primary forest. Shown are results of an ANCOVA with distance to primary forest and canopy cover as covariates. Significance levels are * $P < 0.05$, ** $P < 0.01$.

		Liana regeneration density		% fibrous lianas of liana regeneration		% lianas of woody regeneration		Species richness		Fisher`s Alpha		Generative regeneration (%)		Vegetative regeneration (%)	
Source of variation	df	MS	F	MS	F	MS	F	MS	F	MS	F	MS	F	MS	F
Canopy cover	1	38.4	0.07	1.465	0.78	0.240	0.01	10.51	0.35	24.12	0.52	1.729	4.27	529.5	1.26
Distance (log)	1	1524.5	2.66	5.941	3.16	191.3	9.98**	354.2	11.83**	46.79	1.01	0.173	0.47	984.6	2.35
Secondary forest type	1	95.7	0.17	0.033	0.02	0.957	0.05	77.97	2.61	89.89	1.94	1.063	2.62	708.5	1.69
Residuals	14	5179.0		1.878		19.17		29.93		46.37		0.405		418.8	

Diversity of regeneration

One hundred and sixty-seven morphospecies and species were found, and both categories were consequently termed 'species'. Fifty percent could be assigned to species level and another 37% to genus level. Thirty-nine percent of all species belonged to two plant families: Bignoniacaea (22%) and Fabaceae (17%). Species richness at the plot level was highest in the primary forest (26 species per 135 m^2 plot) followed by *Cecropia* forest (19 species per plot), and *Vismia* forest (13 species per plot). Only the difference between *Vismia* and primary forests was statistically significant (Table 3.2). When species richness was accumulated over all plots for one forest type, the primary forest and *Cecropia* forest had similar absolute species richness after eight plots (equals 0.11 ha): 95 and 93 species respectively, the *Vismia* forest had 62 species (Figure 3.2). None of the species-area curves seemed to level off.

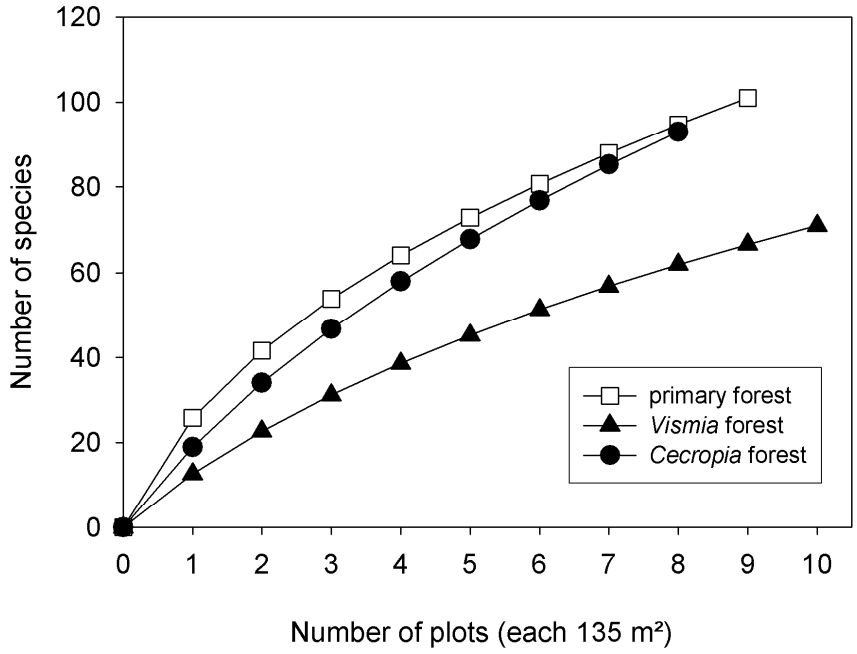

Figure 3.2.
Cumulative species-area curve of liana regeneration (≤ 1.7 m in length) for plots of primary forest and two types of secondary forest. Each plot had an area of 135 m². Species numbers are the average of random subsampling of all plots.

In *Cecropia* forest, the number of individuals was low, and species numbers were medium per plot, resulting in a higher Fisher's alpha (14.3) compared to the primary (10.2) or *Vismia* forest (7.4), but the differences were not statistically significant (Table 3.2). Species richness was influenced by the distance to the primary forest but not by canopy cover. Species richness decreased with increasing distance to the primary forest ($R = -0.647$, $df = 17$, $P > 0.01$). The difference between secondary forest types was insignificant. Fisher's alpha was not influenced by distance or canopy cover as a covariate (Table 3.3).

The most abundant species per forest type, which made up 50% of the individuals, hardly overlapped between forest types. *Derris floribunda* (Benth.) Ducke was very abundant in the primary forest, but also in some *Cecropia* forest plots. The two secondary forests shared *Doliocarpus dentatus* (Aubl.) Standl. and *Odontdenia* sp. A as the most abundant species (Table 3.4). In the primary forest, six plots were clearly dominated by a single species, and species identity differed from plot to plot. Each of the five abundant species listed in Table 3.4 dominated a single plot, while *Derris floribunda* dominated two plots. *Ampelozizyphus amazonicus* Ducke and *Machaerium* sp. P occurred, in addition to the plot they dominated, in two to three other plots but only with one to two individuals.

The most frequent species in the primary forest were *Abuta rufescens* Aubl., *Rourea cuspidata* Benth. Ex Baker, and *Paullinia* sp. A. They all occurred in every plot and were moderately abundant. In the secondary forest the most frequent species was *Doliocarpus dentatus*, which occurred in nine *Vismia* forest plots and seven *Cecropia* forest plots, followed by *Odontadenia* sp. A that was found in five plots (Table 3.4). Both species were also among the most abundant. In the *Cecropia* forest, *Arrabidaea egensis* Bureau & K. Schum. was another frequent species (five from eight plots). In the *Vismia* forest, *Mikania* sp. was present in six out of 10 plots.

The density of the most abundant species, which occurred in several plots of secondary forests was not correlated with distance to the primary forest. Only for *Aristolochia rumicifolia* Mart. & Zucc., there was a weak tendency for the abundance per plot to be negatively correlated with distance ($R = -0.660$, $df = 8$, $P = 0.053$).

Table 3.4. The most abundant species that made up around 50 % of liana regeneration accumulated per forest type. Species are ordered in abundance rank, despite overlap between forest types. ind = individuals summed up across all plots per forest type, plot= number of plots per forest type in which the species occurred. The three most frequent species of liana regeneration per forest type are marked with (freq) when overlapping with abundant species. Plot numbers *n* = 9, primary forest; *n* = 8, *Cecropia* forest; *n* = 10, *Vismia* forest.

primary forest			Secondary forest					
			Cecropia			*Vismia*		
species	ind	plot	species	ind	plot	species	ind	plot
Derris floribunda	251	3	*Derris floribunda*	25	2			
Ampelozizyphus amazonicus	149	3						
Machaerium sp. P	110	3						
Maripa glabra	93	6						
Paullinia sp. A (freq)	66	9						
			Adenocalymna subicanum	31	4			
			Mimosa guilandinae var. 2	31	2			
			Arrabidaea sp. A	28	1			
			Memora adenophora	23	3			
			Doliocarpus dentatus (freq)	19	7	*Doliocarpus dentatus (*freq)	34	9
			Odontadenia sp. A (freq)	15	5	*Odontadenia* sp. A (freq)	67	5
			Acacia altiscandens	11	3			
			Memora moringiifolia	10	2			
			Aristolochia rumicifolia	10	4			
						Senna tapajozensis	43	4
						Mikania sp. (freq)	35	6
						Davilla sp. H	25	3
						Malpighiacaeae sp. R (cf *Mascagnia)*	25	3

Discussion

Density of tall lianas and liana regeneration

The stem density of tall lianas in the primary forests found in our study (320 ± 100 SD stems ha^{-1} ≥ 2 cm) only slightly deviates from an earlier study (400–500 stems ha^{-1} ≥ 2 cm diameter) in primary forests of terra firme regions in central Amazonia (Laurance et al. 2001). Earlier studies have found that liana stem density decreased with forest age. In a chronosequence study in central Amazonia tall liana stem density has been found to decrease with forest age and was lowest in primary forests (Gehring et al. 2005). In Panama, the density of lianas in 20–40 years old forest was twice as high as in old-growth forests (DeWalt et al. 2000). In the lowlands of Costa Rica, highest liana stem densities (c. 1500 stems ha^{-1} ≥ 0.5 cm) were observed in young secondary forest (< 15–20 years old), with a decrease in older secondary forests, and lowest densities in the old-growth forest (Letcher and Chazdon 2009). Compared with the latter study, our secondary

forests were of similar age and had lower stem densities of lianas in the *Vismia* forest (mean 912 stems $ha^{-1} \geq 0.5$ cm diameter), and higher densities in *Cecropia* forest (mean 2147 stems $ha^{-1} \geq 0.5$ cm diameter). Frequent fires during former land use as pasture land may be one reason for the relatively low density of lianas in *Vismia* forests, as Gerwing (2001) showed that burning was an effective treatment for liana density reduction. In contrast, lianas in *Cecropia* forest could resprout from fallen stems. The differences in stem density of tall lianas between *Vismia* and *Cecropia* forest, as observed in our study, emphasise the importance of previous land use for the abundance of lianas in secondary forests.

We found a relatively low abundance of middle-sized lianas when compared with tall lianas and with liana regeneration density. Such a diameter-density distribution was earlier observed by Putz (1984) in a Panamanian old-growth forest. He observed that lianas of intermediate size classes (8–24 m) were missing and suggested that seedlings were not successful in climbing up through the mature forest.

The density of total woody regeneration in the primary forest found in our study was somewhat lower than results of previous studies in the region: we found eight plants m^{-2}, whereas Benítez-Malvido and Martínez-Ramos (2003) found 15 plants m^{-2} in continuous forest, and Sizer and Tanner (1999) observed 13–16 plants m^{-2} in large forest fragments. In our study, the share of lianas in woody regeneration (10–13%) was lower when compared to previous findings in other old growth forests: in the slightly drier eastern Amazon, lianas contributed 19% of regeneration (< 2 m) (Gerwing and Farias 2000), and 20–30% in lowland forest in Panama (Putz 1984, Schnitzer and Carson 2001). In secondary forests, we encountered only half the number of woody regeneration including lianas than in primary forests. In forests of comparable age on abandoned pastures in Costa Rica, liana seedlings contributed between 6–12% of woody regeneration and decreased within a chronosequence from 13 to 26 years (Carpers et al. 2005).

In our study, the secondary forest differed from the primary forest in total abundance of liana regeneration, but not in the share that lianas contributed to total woody regeneration. The share of lianas in secondary forests decreased with increasing spatial distance to primary forest, whereas the total woody regenerations density remained similar. This suggests that lianas did not have an advantage compared to other woody growth forms during establishment and growth in secondary forests. Comparing only the abundance of trees and lianas, lianas had a higher share in the *Vismia* forest (19%) than in the other forests (14% in primary forest and 15% in *Cecropia* forest). A seedling study in the same primary forest (BDFFP area) found tree seedlings to be 120 times more abundant than lianas (Benítez-Malvido and Martínez-Ramos 2003). The authors of that study

reported a total of two lianas in 20 m² (much less than in our study), however methodological differences limit comparability. The *Vismia* forest had the highest share of fibrous lianas (17% in *Vimsia* forest, 8% in *Cecropia* forest, 2% in primary forest). These plants are likely to be short-lived and possess pioneer characters, thus decrease in abundance during succession. Aside from the described differences in fibrous lianas, neither density nor percentage of liana regeneration was affected by the land use history of the two secondary forest types.

The mode of regeneration differed among forest types. In the primary forest, where seed sources from seed rain or seed bank can be assumed to be high, regeneration from seeds was dominant (55%). The *Cecropia* forest had few seedlings, and a high percentage of regeneration was of vegetative origin (63%). Sprouts from fallen stems and a vegetative net in the ground are probably the primary source of regrowth for lianas in this forest type. The areas, that were now covered by *Vismia* forest, had experienced intensive repeated fires before the forest established, and one would expect that regeneration mainly originated from newly dispersed seeds. A former study in the Bolivian tropical dry forest reported that high intensity fires reduced vine regeneration and the share of sprouts on regeneration (Kennard et al. 2002). Still, the regeneration mode was fairly mixed in *Vismia* forest. The unexpectedly high percentage of vegetative regeneration could be due to the abundance of *Odontadenia* sp. A, *Mikania* sp. and the Malpigiaceae species in the *Vismia* forest plots. Though now spreading mainly by vegetative means, it is very likely that these species originally established on the sites through their wind dispersed seeds. The adjacent primary forest may represent an important seed source for regeneration in secondary forests, but in our study no correlation between distance to primary forest and share of generative regeneration was uncovered.

Diversity

In contrast to the outstanding high and much better explored tree diversity, liana species richness of the central Amazon is considered intermediate and comparable with the African lowland forest (Gentry 1991a). Close to Manaus, 300 liana species were identified in a 10 km x 10 km reserve (Reserva Ducke, Ribeiro et al. 1999). In the primary forest of our study area, earlier surveys found 13 species ha^{-1} of big stemmed lianas (diameter ≥ 10 cm) on flat terrain (Oliveira et al. 2008), 83 species and morphospecies for stems ≥ 2 cm diameter in 2.9 ha (Laurance et al. 2001), in which subsamples of 1 ha averaged c. 70 species. Gentry (1991a) counted on average 39 species per 0.1 ha for stems > 2.5 cm diameter in several sites of Amazonian lowland forest.

In the present study we considered liana species numbers only of regeneration. Considering the species-area curve, which was made by random subsampling of plots, the studied primary forest had c. 95 species of liana regeneration per 0.1 ha (Figure 3.2). The number is probably an overestimation due to difficulties in the identification of immature, small plants and singletons. Including this uncertainty we found twice as many species in the primary forest as Gentry (1991a) counted at several sites in Amazonian lowland forest for bigger-sized lianas. However, this difference may also be partly explained by our inclusion of many species that never reach a diameter of 2 or 2.5 cm. The inclusion of such thin stems in surveys of liana communities naturally accounts for higher diversity (Hegarty and Caballé 1991).

Species richness per plot was highest in primary forest and lower for secondary forests but did not significantly differ between secondary forest types. A high diversity for *Cecropia* secondary forest was indicated by Fisher's alpha. This was further suggested by the aligning of the species area curves which resulted in similarly high values for primary and *Cecropia*-dominated secondary forests, whereas the *Vismia* forest had a shallower curve progression. The high diversity could be due to the co-occurence of old-growth as well as secondary species in some *Cecropia* plots, which were located close to primary forests. This suggestion would be supported by the fact that species richness decreased with distance to primary forest. However, no such relation could be found for Fisher's alpha. Yet, studies of tall lianas suggest that diversity is either similar or higher in secondary forests than in old-growth forest (DeWalt et al. 2000, Letcher and Chazdon 2009). Combining the results of both methods, we suggest that species richness of liana regeneration in our study was similar in the primary and *Cecropia* forests and that the *Vismia* secondary forest had lower species richness and diversity. Besides species numbers, species community differed between all three forest types, although we considered only the most abundant species and did not use similarity indices or ordination. Both secondary forests shared

two very abundant species, the other common species varied in identity and also in growth form, e.g. *Mikania* sp. and the Malpighiacaeae species, both common in the *Vismia* forest, were considered as fibrous.

Conclusions

The main findings of our study on liana regeneration in two types of secondary forest and in primary forest of central Amazonia are as follows:

- Density of liana regeneration was significantly higher in primary forest compared to both types of secondary forests.
- Highest species richness per plot was found in the primary forest and lowest in the *Vismia* forest. Accumulated species richness in the *Cecropia* forest was similar to that in the primary forest.
- Generative regeneration occurred predominantly in primary forest whereas vegetative regeneration was prominent in *Cecropia* forest.
- Secondary forest that established directly after a clear cut had twice the stem density of tall lianas as secondary forest on former pasture land. However, for liana regeneration, our data could not confirm this difference in density between secondary forest types. Nevertheless *Vismia* forest had a slightly higher percentage of fibrous lianas, and *Cecropia* forest more vegetative regeneration than the other forest type, respectively.
- Compared to *Cecropia* secondary forest with no pasture history, *Vismia* forests, which had experienced intense land use, including fire, exhibited lower species richness and partly other abundant species of liana regeneration in succession.
- Increasing distance to primary forest also decreased species numbers and the share of lianas on woody regeneration. The effect of land use history or distance could not be untangled in our study.
- Canopy cover of secondary forest had no influence on any measured values of liana regeneration.

So far it is difficult to identify where and when lianas benefit in the course of secondary forest succession, which includes deterministic but also stochastic processes (Chazdon 2008).

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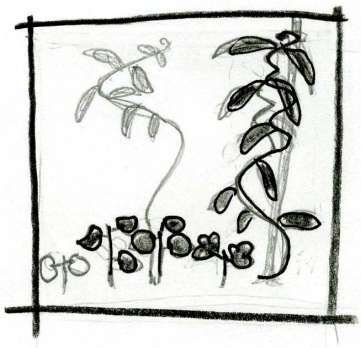
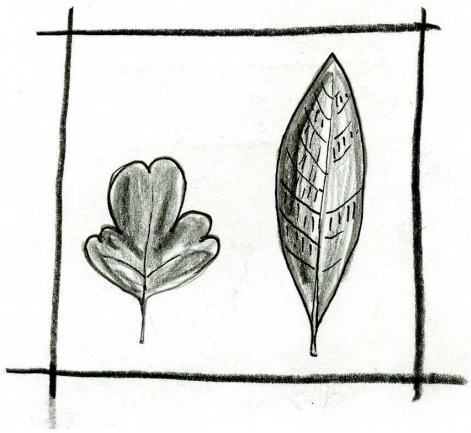
4. Traits and Growth of Liana Regeneration in Primary and Secondary Forests

M Roeder, D Hölscher, IDK Ferraz





Abstract

Lianas are considered to be particularly abundant in tropical forests after disturbance, however information on liana seedlings, saplings, and sprouts is scarce. We assessed plant functional traits as well as growth rates of liana regeneration (≤ 1.7 m length) in two secondary forest types in comparison to primary forest. The study was conducted near Manaus, Brazil, and secondary forest types were: *Vismia* (on land formerly clear cut, used for pasture and intensively burned) and *Cecropia* (no pasture usage or intensive fires after clear cut). A principal component analysis suggested that the majority of the primary forest species exhibited a similar habit and were characterized by short shoots and small, round leaves with low specific leaf area, whereas secondary forest species had a broad range of trait values. At the plot-level, separation of primary and secondary forest communities was confirmed with plant length and leaf size being the most influential traits. Plant size varied more within secondary than within primary forest plots. The two secondary forest types could not be separated into two groups based on their traits of liana regeneration. Herbivory increased and variability of leaf size and plant length per plot decreased with increasing canopy cover. Relative growth rate (RGR) did not correlate significantly with any measured plant trait, except for a negative relation to initial length. RGR increased with decreasing canopy cover and was highest in *Vismia* forest plots. We concluded that plant functional characteristics of liana regeneration were more converged in the primary forest and differed substantially from secondary forests, yet canopy cover explained only partly the observed differences.

Introduction

Lianas are an important component of tropical forests. They contribute around 25 % of the stem density and diversity of woody plants in many tropical lowland forests (Schnitzer & Bongers 2002) and influence the biological dynamics of a forest in various ways. Natural disturbances and anthropogenic activities have been documented to increase liana abundance such as in tree fall gaps, forest borders, forest fragments and secondary forests (Schnitzer et al. 2000, Laurance et al. 2001, Letcher & Chazdon 2009). Therefore, lianas are often regarded as light-demanding growth forms. On the other hand a lot of species are known to persist in the understory of old grown forest and are shade tolerant at least in the regeneration stage (Putz 1984, Gerwing 2004). Although lianas can be easily distinguished from other growth forms in the adult stage, the habit of seedlings and saplings ranges from tree-like, self-supporting plants to delicate, thread-like seedlings that are obligate climbers. The habit of one seedling can change with environment cues (e.g. sudden light availability) and time.

Differences in habit and seedling performance can be described by traits and shed light on the functional diversity of growth forms or species in a community. Analyses of traits has gained importance in ecological research over the last few decades and many studies have been conducted in different biomes (e.g. Chapin et al. 1996, Garwood 1996, Ackerly et al. 2002, Poorter & Bongers 2006) or even across biomes (e.g. Wright et al. 2004b). Performance of seedlings was found to be closely related to several leaf traits (e.g. Reich et al. 1992). The most obvious difference of performance in plant regeneration is the trade-off between growth and survival, resulting in persistent, slow growing species with high survival rates on the one hand and fast growing species with low survival rate on the other hand. However, the whole continuum between these extremes in trade-offs exists (e.g. Gilbert et al. 2006). Trait values might serve as predictors of the success of a species in different environments and different trait combinations may allow coexistence of species in the same environment. In the ideal scenario, traits that are easy and fast to obtain may be able to predict whether a species will, for example, be able to establish under low light conditions or whether it will be successful in disturbed areas. Trait data also offer the possibility to describe main features of a plant community without the need for species identification. This could be a very helpful approach particularly in tropical environments, due to the high diversity and the scarcity of knowledge on some groups such as lianas.

With the increase of disturbed areas in tropical regions e.g. secondary forest or fragmented forests, the density of lianas is expected to increase. However, species with trait combinations resembling pioneers might in the main part benefit from these areas and liana infestation will also

be influenced by land use history, for example intensive fires. Studies on the regeneration of lianas in secondary and primary forest are in general scarce; performance and traits of seedlings and sprouts have barely been studied. One study of seedling and sapling performance in primary and secondary forest of Panama (BCI) indicated that lianas and tree seedlings had widely overlapping ranges in growth rate and survival (Gilbert et al. 2006).

We investigated the following main questions: Do traits of liana regeneration differ in secondary forest types of varying land use history and primary forest? Is the variability of traits and growth different in the forest types? To answer these questions, we used traits related to whole plant habit and leaf morphology as well as herbivory and relative growth rate during one year of liana seedlings, saplings and sprouts. Traits on community and species level were investigated in primary forest and in the two main types of secondary forest found in the region, central Amazon, Brazil. The two secondary forest types resulted from different intensities of former land use. If clear-cut land was used for cattle ranching and intensely burned, a secondary forest dominated by trees from the genus *Vismia* developed (Mesquita et al. 2001). If the primary forest was only clear cut and not intensively burned, initially the genus *Cecropia* dominated, and the subsequent tree species assemblages were more diverse than in the *Vismia* forest (Mesquita et al. 2001).

Study site

The study was conducted in the area of the Biological Dynamics of Forest Fragments Project (BDFFP) (Lovejoy & Bierregaard 1990), north of Manaus, Brazil (2°20-25´S, 60°W). The annual rainfall in Manaus averages 2285 mm (INMET 2010) with a June-October dry season. The mean annual temperature is 26.7 °C (Lovejoy & Bierregaard 1990, Laurance 2001). Soils were classified as nutrient poor acidic xanthic ferralsols (Ranzani 1980, FAO 2003) with high clay content and drain well (Chauvel 1987, Laurance et al. 1999). Elevation ranges from 50 - 100 m asl and topography consists of plateaux and deeply dissected valleys. Mature vegetation is evergreen, non-inundated (terra firme) lowland tropical forest with trees 35 - 40 m tall (Rankin de Mérona *et al.* 1992). Density of trees is on average 613 stems ha^{-1}, ≥ 10 cm diameter at breast height (DBH) (Laurance 2001). Tree diversity is high with more than 1000 species in the area (Rankin de Mérona et al. 1992, Ribeiro et al. 1999, Laurance 2001) and 280 species ha^{-1}≥ 10 cm DBH (Oliveira & Mori 1999).

The area of the PDBFF includes primary forest and, at time of the study, 17 - 25 year old secondary forest which established after clear cut. According to Mesquita et al. (2001), two main types of secondary forests (*Vismia* and *Cecropia* forest) developed in the area: *Vismia* forest established when areas were used as cattle pasture for about four years and experienced repeated intense fires. At the beginning of our study (2007), the secondary forest in these areas was 17 to 19 years old (T. Vizcarra, pers. com.) and dominated by the genus *Vismia* (Clusiaceae) and species of the Melastomataceae family. In areas that experienced few or no fires and no cattle ranching, initially a forest dominated by *Cecropia* (Urticaceae) developed. This forest type of about 25 years old was characterized in 2007 by greater tree species diversity than the *Vismia* forest and few living *Cecropia* trees remained, however it will be consequently referred as *Cecropia* forest.

Material and Methods

Study plots

Plots were established at four sites which had ~40 km to ~8 km distance to each other. Initially 18 secondary forest plots (ten *Vismia* and eight *Cecropia)*, and nine primary forest plots were studied, later on three (in growth analysis four) plots were excluded from analysis due to small plant sample size. Plots of the same forest type were always distributed over three sites and within a site had 0.5 km – 3 km distance to each other. Distance to primary forest was between 25 m and 1200 m for secondary forest plots. A plot consisted of three long subplots (1.5 m x 30 m) with 1.5 m distance to each other, resulting in a total plot area of 135 m². Stand structural characteristics of all three forest types and data on soil properties are provided in Table 4.1. Details on soil analysis methods are described elsewhere (Roeder et al. in press). A detrended component analysis (DCA) of log-transformed tree family data from stems ≥ 5 cm DBH confirmed the separation of the secondary forests into two groups. Eigenvalues were 0.48 for the first axis and 0.21 for the second. Together the two axes explained 35.4% of the total variance. Clusiaceae and Melastomatacea correlated with first axis with R = 0.82 and R = 0.76 respectively. *Vismia* forest had significantly lower values of canopy cover (0.74) than *Cecropia* or primary forest (both 0.87) (Table 4.1).

Study species

During the survey of liana regeneration in all 27 plots more than 160 species or morphospecies including many single- and doubletons were found within 2319 plants, details are described

elsewhere (Roeder et al. in press). Species richness as well as regeneration density per plot was highest in primary forest (Table 4.1). For the present study, the 26 most important species (including morphospecies) were chosen, which covered 72% of all measured plants. Importance was calculated as modified importance value index, IVI (Kershaw & Looney 1985) as relative abundance + relative frequency and species with IVI ≥ 2 were included (Appendix 4.1). Sample size per species was between 17–286 plants, in total 1542 plants were used. Many species were spatially clumped and occurred only in one or two plots. Species were assigned to a main habitat (primary, *Vismia* or *Cecropia* forest) when two-thirds of plants occurred in one habitat type; otherwise species were regarded as co-occurring. When traits were examined per plot, only plots that contained at least fifteen plants of the 26 most abundant species were included, resulting in 24 plots with 15–209 plants. Per forest type, plots were still distributed over three sites, repetitions were *Vismia* = 8, *Cecropia* = 7, primary forest = 9 plots. Species richness and regeneration density was still significantly different between forest types with the reduced data set.

Table 4.1. Forest structure and soil properties (mean +/- 1 standard deviation) of the studied primary and secondary forest types near Manaus, central Amazon. Lowercase letters indicate significant differences ($P < 0.05$) in ANOVA followed by Tukey post-hoc HSD test for each row. Tree height was compared with T-Test, † = literature data (Rankin de Mérona et al. 1992).

	primary forest	secondary forest	
		Cecropia	*Vismia*
initial number of plots	9	8	10
tree basal area (≥ 10 cm dbh, m²/ha)	33.2 ± 16.6 a	20.1 ± 5.7 b	16.5 ± 7.4 b
tree height (≥ 10 cm dbh, m)	35-40 (some 45)†	22.4 ± 2.8 a	17.7 ± 2.3 b
tree stem density (≥ 10 cm dbh n/ha)	721 ± 191 a	639 ± 184 a	756 ± 353 a
tree stem density (< 10 cm dbh n/ha)	6524 ± 1803 a	5417 ± 1917 a	6169 ± 3356 a
cover fraction of canopy	0.87 ± 0.03 a	0.87 ± 0.05 a	0.74 ± 0.05 b
density of liana regeneration (n/plot)	142 ± 64 a	51 ± 21 b	46 ± 27 b
species richness of liana regeneration (n/plot)	26 ± 5 a	19 ± 7 ab	13 ± 7 b
mineral soil (0-10 cm)			
total N (g/kg)	1.4 ± 0.5 a	1.9 ± 0.6 a	1.7 ± 0.3 a
P (Mehlich extraction) (mg/kg)	3.5 ± 0.6 a	4.1 ± 1.2 a	3.1 ± 0.8 a
K (Mehlich extraction) (mg/kg)	22.4 ± 5.8 a	27.3 ± 6.4 a	25.1 ± 4.9 a
pH in H_2O (median)	4.1	3.9	4.1
soil texture	loamy sand	loam	clay loam

Traits

From April to July 2007 all individually rooted liana seedlings, saplings and sprouts (≤ 1.7 m in length) were marked, identified, and the length, number of leaves, length and width of the biggest leaf were measured. After twelve months (May to July 2008), all plants were surveyed again and also all overseen or new plants were included. Additionally, the diameters at the base (d_1), in the middle (d_2) and below the last leaf (d_3) were measured, the herbivory per leaf was estimated and the biggest, fully developed leaf was harvested for determination of specific leaf area. Seven traits, describing leaf and plant habit, were used:

(1) *Plant length* – maximum shoot length of plant, upper limit 1.7 m.

(2) *Leaves per length*- leaf number of whole plant (incl. all branches) divided by maximum shoot length.

(3) *Leaf size* – Leaf size was leaf width x length x 2/3 (Cain & Castro 1959). In case of composed leaves, only the biggest leaflet was used. The term is used to differentiate from leaf area, where all leaflets were included.

(4) *Width/length ratio (WLR)* – WLR was width divided by length of the leaf. In case of composed leaves, only the biggest leaflet was used. Contrasting to the mechanical measured leaf area for the specific leaf area (SLA), length and width of the biggest leave measured in the field were available for every plant. WLR describes if leaves are elongated or round.

(5) *Specific leaf area (SLA)* – The biggest and fully developed leaf of a plant was scanned with an area meter (Li 3050A, Li-Cor, Lincoln, Nebraska, USA), while in full turgor, and afterwards dried at 80 °C for 2 days and weighed to 0.1 mg accuracy. In case of compound leaves, all leaflets were included and the mid vein was excluded. SLA was area divided by weight (m^2/ kg). For very abundant species a maximum of 10 leaves were sampled per species and plot. When analysed per plot, missing values were completed by mean SLA (all plots) of the species. SLA is a measurement of leaf thickness or tissue density.

(6) *Herbivory* – Damage of every leaf per plant was estimated in the field. Leaves were assigned into five groups: no damage (0 %), 1–10%, 11–25%, 25–50%, 50–100% damage. The leave damage (LD) was calculated as

$$\mathrm{LD}=\sum_{i=1}^{4}\frac{n_i\,(c_i)}{N}$$

where n = number of leaves in category i, c = midpoint of category e.g. c_4 = 75%, N = number of leaves on the plant. Heavy leaf damage due to fungal infestation was treated as herbivory (adapted from Morrow 1984 and Benítez-Malvido et al. 2005). Herbivory should be reduced when leaves are hard structured or accumulate high secondary compound contents, which is often the case in long lived leaves and slow growing plants.

(7) *Ratio of stem slenderness (RSS)* – Based on the ratio of slenderness used in engineering (e.g. Kuhlmann 2004), the relation of diameter to stem length was calculated, as length divided by the mean of the three diameters d_1, d_2, d_3. RSS reflects the gradient between free standing and support needing plants and also influences persistence of a plant.

Relative growth rate

Performance of seedlings and sprouts was described by relative growth rate (RGR). Calculation followed Hunt (1990)

$$\mathrm{RGR} = \frac{\ln H_{t2} - \ln H_{t1}}{t_2 - t_1}$$

where H_{t2} = height (here length) at t_2 in cm and H_{t1} = height at t_1, t_1 = time of the first measurement and t_2 = time of the second measurement, which was in the present study 1 year. For the analysis the data set had to be reduced to 22 species because replicates were lower than ten plants for some species in 2007; in total 1040 plants were analysed with 10–259 plants per species. Individuals that died during the year were excluded; annual mortality was 4.9% during the study period. The RGR per plot, on the basis of the 22 species data set, was used in 23 plots with 14–185 plants. Four plots, which had less than ten plants, were excluded. Per forest type plots were still distributed over three sites, repetitions were *Vismia* = 8, *Cecropia* = 6, primary forest = 9 plots. Since some variables were only measured in 2008 (SLA, RSS, herbivory), and the other variables were highly correlated between years ($R > 0.84$, $P < 0.001$, mean per species), only values of 2008 (but of the corresponding smaller dataset of 22 species) were used for correlation with RGR, though we included initial plant length of 2007 in the analysis.

Canopy coverage

In each plot, five hemispherical photographs were taken with a digital camera (Nikon coolpix 4500) equipped with a fish eye lens (Nikon FC E8 0,21x) and mounted on a tripod. The pictures were taken on the mid-line of the plot at a height of 0.73 m above the ground and at a distance of 5 m from one point to the other. The hemispherical pictures were analyzed for cover fraction of the canopy (f-cover) using the programme CAN_EYE V5 Hem (INRA, Avignon, France).

Data analysis

The arithmetic mean per species (or per plot) was calculated for the seven traits (length, SLA, herbivory, WLR, leaf size, RSS, leaves per length) and relative growth rate. As a measure of the variability of traits within a plot, standard deviation (SD) was used. Data was $\log_{10}$ transformed if necessary to reach normal distribution. Pearson's correlation was used for the correlation matrix of traits and the relationship between traits, canopy cover and growth rates. Differences between forest types were verified via one-way ANOVA. Prior principal component analysis (PCA), the untransformed data were centralized and standardized. Significance level was set at $P < 0.05$. Analyses were carried out using R-2.8. 1 (R Core Developement Team 2009), for multivariate statistic PCOrd 5.0 (mjm software, Gleneden Beach, OR, USA) was used.

Results

Traits per species

Differences between species. Species differed significantly in the studied traits (seven ANOVAs, all F > 5.5, and all $P < 0.001$); it was not verified which species contrasted with another. Mean values of six traits varied between two fold for WLR (0.259 cm/cm for *Adenocalymna subicanum* and 0.543 cm/cm for *Paullinia* sp. A) and nine fold for leaves per height (0.086 n/cm for *Maripa glabra* and 0.745 n/cm for *Cheiloclinium hippocrateoides*). Leaf size had the biggest variation between species (88 fold variation), and ranged from a leaflet size of 1.1 cm² (*Machaerium ferox*) to leaf size of 100.4 cm² (*Adenocalymna subicanum*). See Appendix 4.1.

Correlation of traits. Four pairs of traits correlated significantly over the 26 species. The ratio of stem slenderness (RSS) increased with increasing plant length and also with increasing SLA, whereas number of leaves per stem length decreased with increasing RSS. These correlations were mainly driven by three very delicate, always climbing species (*Dicranostyles scandens, Maripa glabra, Aristolochia rumicifolia),* which had high slenderness ratios. Leaf size decreased with increasing width-length ration of the leaf, meaning that small leaves were rounder (Table 4.2).

Table 4.2: Pearson's correlation coefficient (R) of leaf and plant traits of 26 liana species in the central Amazon, Brazil. Significant correlations ($P < 0.05$) are bold. SLA = specific leaf area, WLR = width-length ratio of a leaf, RSS = ratio of stem slenderness.

trait (mean per species)	leaf area	leaf/ length (log)	herbivory (log)	length (log)	SLA (log)	RSS (log)
leaves per length (log)	0.165					
herbivory (log)	0.160	-0.108				
plant length (log)	0.344	-0.085	0.094			
SLA (log)	-0.368	-0.249	-0.142	0.097		
ratio of slenderness (log)	-0.098	**-0.442**	-0.256	**0.436**	**0.530**	
WLR (log)	**-0.477**	-0.201	0.008	-0.324	0.022	-0.326

Ordination of species traits. The first axes of the PCA explained 29% of variation of the studied traits between species. It related to the traits SLA and slenderness (positively) and to leaf size and leaves per length (negatively). The second PCA axis explained 27% of variation and was mainly determined by WLR and plant length. Most primary forest species were found in one cluster that

was characterized by round leaves and short growth. Secondary forest species were more scattered in the ordination plot than primary forest species. One group of secondary forest species (exception *Cheiloclinium hippocrateoides*, a primary forest species) could be separated and described as tall plants with abundant, big, elongated leaves. Three species from primary and secondary forest (*Dicranostyles scandens, Maripa glabra, Aristolochia rumicifolia*) formed a distinct, isolated group: they all had long delicate, winding stems (low ratio of slenderness) with scarce foliation. See Fig. 4.1a.

Traits per plot

Influence of forest type and canopy cover. Mean values of traits per plot differed between forest types in four cases: Liana regeneration had longer shoots and bigger leaves in *Cecropia* forest than in primary forest, plants had more leaves per length in the *Vismia* forest than in primary forest and herbivory was higher in *Cecropia* than in *Vismia* forest (all $F > 3.7$, $P < 0.05$). Variability of traits within a plot (here expressed as SD) was significantly smaller for plant length and leaf size in the primary forest than in the two secondary forest types. SLA was higher in *Vismia* than in primary forest (all $F > 4.8$, $P < 0.05$, Table 4.3). Canopy cover and trait variables correlated in two cases: Herbivory increased with higher canopy cover and the variability of leaf size was higher when canopy cover decreased (Table 4.4).

Ordination of plot traits. The ordination of traits on plot level (mean per plot) gave a result similar to the ordination of species traits, although axes were rotated by 90%. The first axis (33%) was mainly determined by the length of the plant, leaf size and WLR, while the second axis (24%) was determined by leaves per length (Fig. 4.1b). Most primary forest plots formed one cluster, characterized by a trait combination of short length, small and round leaves and few leaves per length. Five out of six *Cecropia* forest plots had intermediate values for most traits and therefore clustered in the middle of the ordination graph. *Vismia* forest plots were widely scattered in the ordination.

Ordination of plot trait variability. The first axis explained 37% of variation, the second axis 18%. Standard deviation of plant length, of SLA and of ratio of stem slenderness correlated positively with the first axis, standard deviation of herbivory and of WLR mainly determined the second axis. Primary forest plots were grouped by low variability of the mentioned influencing traits, whereas standard deviation of traits in secondary forest varied widely. Plots of the two secondary forest types were not separated along the first two axes (Fig. 4.1c).

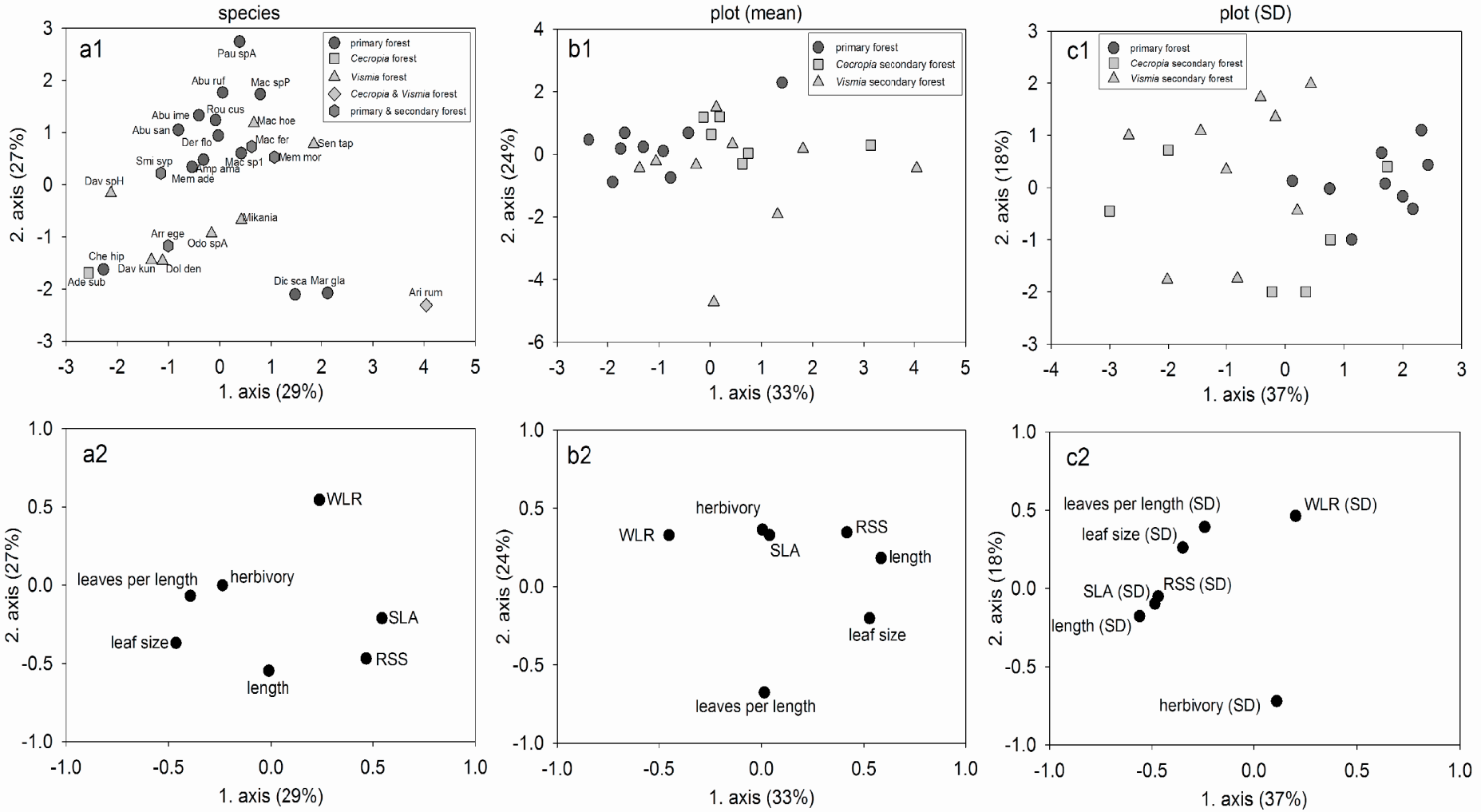


Figure 4.1: Three principal component analyses of seven traits in 26 liana species for trait per species (a1, a2), trait per plot (b1, b2) and variability of traits per plot (standard deviation) (c1,c2). Upper graphs (a1-c1) show scores of species or plots on first and second PCA axes, lower graphs (a2-c2) show loading of traits for the first and second PCA axes. Species abbreviations are found in Table 4.1, WLR = width length ratio of a leaf, SLA = specific leaf area. RSS = ratio of stem slenderness. Main habitat of species is indicated by varying symbols. Plots in the same forest type are marked with the same symbols.

Table 4.3: Differences of traits of liana regeneration for three different forest types in the central Amazon, Brazil. Given are the F- and *P*-values of ANOVAs and the significant pairs of the Tukey post-hoc HSD test. We tested the mean of trait values per plot and the variability per plot (standard deviation). WLR = width length ratio of a leaf, SLA = specific leaf area. RSS = ratio of stem slenderness. SLA and leaf size were log-transformed prior to analysis. Sample sizes were: n = 9 for primary forest (PF), n = 7 for *Cecropia* forest (C), n = 8 for *Vismia* forest (V). Significant results ($P < 0.05$) are bold.

	Mean per plot			Variation per plot (SD)		
trait	$F_{2, 21}$	*P*	sig. differences in Post Hoc Test	$F_{2, 21}$	*P*	sig. differences in Post Hoc Test
leaf size (log)	**3.941**	**0.035**	C > PF	**6.428**	**0.006**	C,V > PF
leaves per length	**3.658**	**0.043**	V > PF	2.635	0.094	-
herbivory	**4.938**	**0.017**	C > V	2.147	0.142	-
plant length	**4.720**	**0.020**	C > PF	**16.031**	**> 0.001**	C,V > PF
SLA (log)	0.907	0.419	-	**5.200**	**0.015**	V > PF
RSS	0.188	0.830	-	1.745	0.199	-
WLR	3.244	0.059	-	2.151	0.141	-

Table 4.4: The relationship between canopy cover and trait values of liana regeneration in 24 plots in secondary and primary forest, central Amazon, Brazil. We used Pearson's correlations of the mean value per plot of the indicated traits or the standard deviation (SD) within a plot. WLR = width length ratio of a leaf, SLA = specific leaf area. RSS = ratio of stem slenderness. Bold fonts indicate significant correlations ($P < 0.05$).

	Correlation of canopy cover with				
trait (mean per plot)	r	*P*	trait (SD per plot)	r	*P*
leaf size (log)	-0.317	0.131	SD leaf size (log)	**-0.482**	**0.017**
leaves per length	-0.371	0.074	SD leaves per length	-0.311	0.139
herbivory	**0.420**	**0.041**	SD herbivory	0.273	0.197
plant length	-0.064	0.764	SD plant length	-0.204	0.339
SLA (log)	-0.203	0.341	SD SLA (log)	-0.289	0.172
RSS	-0.044	0.838	SD RSS	-0.145	0.499
WLR	0.389	0.184	SD WLR	0.303	0.150

Relative growth rate per species

The relative growth rate (RGR) of the 22 studied species was negatively correlated with the initial plant length (r = -0.512, *P* = 0.015). No other correlation of RGR or variability of RGR (SD RGR) and any of the seven measured traits could be found. RGR for most primary forest species was around zero and RGR did not differ between secondary and primary forests species (F = 0.007, *P* = 0.934). *Davilla kunthii* had the highest growth rate (0.4 cm cm^{-1} yr^{-1}). One secondary forest species (*Adenocalymna subicanum*) and one primary forest species (*Abuta imene*) had negative growth rates. When ordered after increasing standard deviation, most primary forest species were on the side of low variabilty and secondary forest species showed higher variability (Fig. 4.2). Four of the five species with the highest variability were secondary forest species. This separation of secondary and primary species regarding variability of RGR forest was confirmed by an ANOVA ($F_{1,18}$ = 5.41, *P* = 0.032). *Smilax syphilitica* and *Memora moringiifolia* could not be assigned to secondary or primary forest and therefore were excluded from this ANOVA.

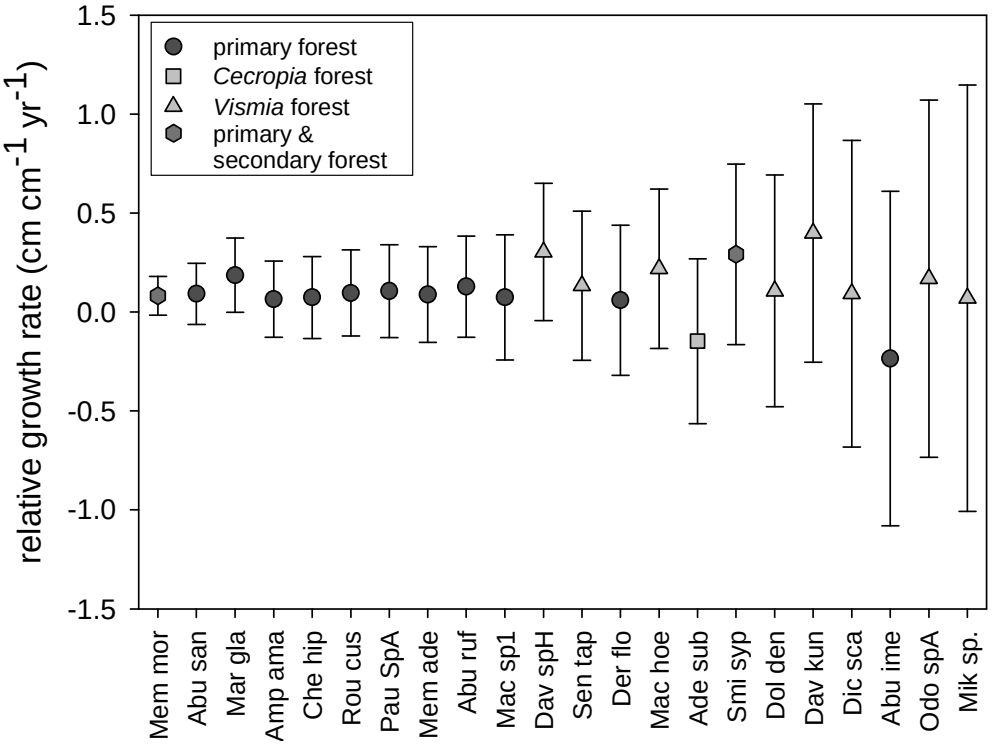


Figure 4.2: Relative growth rate (mean per species) of 22 Amazonian liana species. Mean value and standard deviation are given. Species are ordered according to increasing standard deviation. Main habitats of species are indicated by varying symbols. For species names and sample size see Appendix 4.1.

Relative growth rate per plot

Relative growth rate per plot was different in the three forest types. The *Vismia* forest plots had higher growth rates than plots in primary and *Cecropia* forest. The variability of RGR per plot was lower in the primary forest than *Vismia* forest (Table 4.5). Canopy cover was negatively correlated with RGR (r = -0.507, $P = 0.014$) and but not with the standard deviation of RGR (R = -0.396, $P = 0.061$) (Fig 4.3).

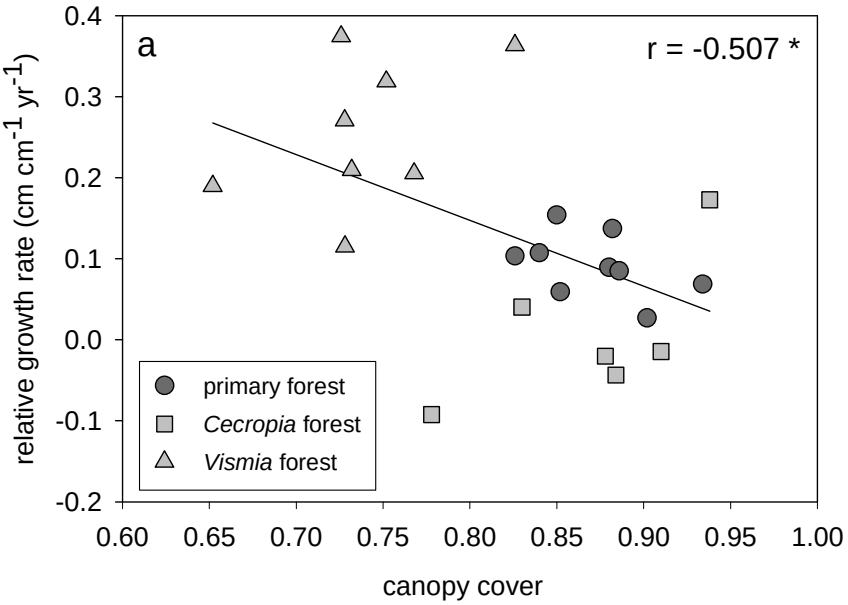


Figure 4.3: Relationship of canopy cover and mean growth rate per plot of liana regeneration in three different forest types in the central Amazon, Brazil. Different symbols indicate different forest types. Replicates (plots) per forest type were: primary forest n = 9, *Cecropia* forest n = 6, *Vismia* forest n = 8. Pearson's correlation was used, significance level is * $P < 0.05$.

Table 4.5: Differences in growth rate of liana regeneration for three different forest types in the central Amazon. Measures were the mean growth rate per plot (RGR) and the standard deviation of growth rate per plot (SD RGR). Given are results of ANOVAs and the significant pairs of the Tukey-post hoc test. Sample sizes were: n = 9 for primary forest (PF), n = 7 for *Cecropia* forest (C), n = 8 for *Vismia* forest (V). Significance level was set at $P < 0.05$.

	Source of variance	df	MS	F	*P*	Significant differences in Tukey Post Hoc Test
RGR (per plot)	forest type	2	0.1151	20.334	< 0.001	V > PF, C
	residuals	20	0.0057			
SD RGR (per plot)	forest type	2	0.193	7.060	0.005	V > PF
	residuals	20	0.027			

Discussion

The separation of primary forest

Traits of lianas in primary forest could be clearly separated from traits in the two secondary forest types at the species level and the community level. Primary forest species were more clumped in the PCA, meaning they had similar trait values whereas species of secondary forest were widely scattered and thus had more heterogeneous trait values. Multivariate analysis of liana communities per plots revealed an even more distinct cluster of primary forest plots. The similar cluster pattern in the ordinations of species traits or plot traits may be explained by the fact that many plots were dominated by only one or two species in the primary forest (pers. observation). The grouping of primary forest species or plots was characterized by short plants with small, round, thick leaves. Correlations confirmed the gradient of species that were short and thick-stemmed with more leaves per length (shrub-like habit) towards long, thin stemmed saplings or sprouts with few leaves (vine-like habit). The ratio of stem slenderness also correlated positively with SLA. SLA, which to a great extent explained the first axis in our ordination of species, is a major predictor of plant strategies: it has been shown to be related with growth rates and traits such as leaf life span, leaf size and nitrogen content of leaves (Reich et al. 1992, Ackerly & Reich 1999, Westoby et al. 2002, Sterck et al. 2006). Low SLA generally occurs in persistent, slow growing plants. Plants with long thread like stems and high SLA should be more vulnerable and less persistent than plants of shrub like habit.

Size-related traits such as length and leaf size were very important in all analyses. The liana community in the primary forest consisted of small plants with small leaves. Size-related features such as plant height and leaf size obviously change with age, especially for seedlings, and are probably not very consistent within a species. However, leaf and twig size has been described as one of four leading dimensions of ecological variation among species (Westoby et al. 2002). In temperate woody species, leaf size increases with plant height (Cornelissen 1999). In a comparative study of tree leaf traits in Indonesian secondary and primary forest stands, mean values of leaf size and SLA were around three and two times higher respectively in secondary than in primary forest communities (Hölscher et al. 2006). Adult lianas do not possess a characteristic height such as freestanding trees. In our case shoot length, which was restricted to an upper limit of 1.7 m, gave an idea about the size of a plant, not necessarily its possible access to light since it could also creep on the ground. Two primary forest species (*Dicranostylens scandens* and *Maripa glabra*) were light foraging (climbing), but most species and individuals in the primary forest could be assigned to the sit-and-wait strategy (Clark & Clark 1992) of shade

tolerant plants. Overall, the liana regeneration in our primary forest plots can be described as a typical shade tolerant community.

Variability and light

Variability also separated secondary and primary forests. Trait values were more consistent in primary than in secondary forests (Fig. 4.1c), e.g. the variability of leaf size, plant length and SLA was significantly lower in primary forest than in at least one secondary forest type. It has to be taken into account however that the variability per plot was also enhanced by the significantly lower plant densities in secondary forest compared to primary forest (Table 4.1). High intraspecific variation in traits may be interpreted as an adjustment to the changing and heterogeneous environmental conditions of successional habitats (Martinéz-Garza et al. 2005); the same might apply for interspecific variation of traits in coexisting species. Increased canopy openness usually goes alongside with increased heterogeneity of light availability. However, in the present study only leaf size variability was increased in plots with low canopy cover and therefore with increased light availability. The understory of primary forest is a more homogenous environment (at a small scale similar to the plot size used in this study) than secondary forest in terms of many environmental variables (e.g. light, temperature) (Richard 1996). Therefore, similar trait combinations and similar performance of plants may be found across primary forest sites.

While *Cecropia* forest and primary forest had similar canopy coverage in most cases, plants were taller or longer, had bigger leaves and showed greater variability in these traits (leave size, plant length) in *Cecropia* as compared to primary forest. Furthermore, *Cecropia* and primary forest plots rarely overlapped in the ordination. This enhances the separation of the different forest types at the trait level. These trait differences probably reflect differences in species compositions, complexity of forest structure, light quality or regeneration mode between these forest types.

The two secondary forests of different past land use (*Vismia* and *Cecropia*) only differed in herbivory and could not be separated from each other in the ordinations. Herbivory was correlated to canopy cover, but, unexpectedly, herbivory was greater in darker forests. According to other findings (Coley 1988), herbivory should be greater in plants with higher SLA and high growth rate, which applies to the *Vismia* forest plots and is in contrast to our findings.

Growth rate

According to expectations, average growth rate per plot correlated positively with increasing light availability, measured here as decreasing canopy cover (Fig 4.3). Canopy cover was significantly lower in *Vismia* forest plots compared to the other two forest types. It was not possible to untangle whether the relative growth rate may have been higher because of better light conditions in the *Vismia* forest, or because the species composing the *Vismia* liana community were characterised by high intrinsic growth rates. In former experiments with subtropical and tropical tree seedlings, early successional, fast growing species had the tendency to have higher RGR than late successional species, also in low light environments (Poorter 1999, Souza & Válio 2003). The variability of growth rates per plot was also high in the *Vismia* forest, indicating that some plants hardly grew at all and others produced metre-long shoots during one year. In primary forest, low RGR and low variability of RGR within a plot completed the picture of persistent, slow growing regeneration.

Growth rates of secondary or primary forest species were not significantly different in our study but most of the secondary forest species showed greater variabilty in RGR than primary forest species. High variation of growth rates may be explained by species-specific high potential growth rates which can reach their maximum in favoured environments, but stay close to zero in unfavoured environments.

Negative growth rates were included in this analysis to capture the actual performance of plants in the different environments and not just the potential growth rate of plants without any growth-reducing factors. The negative growth rates resulted from dieback of shoots due to necrosis or other damage, which should be enhanced in soft, fast grown shoots. Three out of five species with the highest standard deviation of growth rate, which included negative and positive growth, were all climbing and some of them subwoody species (*Mikania* sp., *Odontadenia* sp. A, *Dicransostylens scandens*). This vine-like habit enables fast cheap growth, but also increases vulnerability. The average growth rate in many *Cecropia* plots was even below zero and variability was intermediate between primary and *Vismia* forest. Another reason for negative growth rates beside the mentioned species-specific habits could be as well the higher amount of litter and the falling debris of dying trees in the *Cecropia* forest (pers. obs.).

Leaf and plant traits were not correlated to growth rate in the present study, except for the initial length of plants. This is in contrast with results of numerous former studies of global or local tropical datasets where RGR was related to several leaf traits like leaf life span, SLA,

assimilation rate and nitrogen contents (Reich et al. 1992, Cornelissen et al. 1997, Cornelissen 1999, Cai et al. 2007). Similarly, we did not find support for herbivory correlating with RGR. Coley (1988) found that herbivory rates increase with higher RGR, which can be explained by the fact that long-lived leaves had higher concentrations of immobile chemical defences. However, the comparability is limited because negative growth rates were included in the present study. This should impede a strong correlation with traits widely related to photosynthesis and primary production, but structural traits like stem slenderness could be expected to be correlated.

Conclusion

Traits differed clearly between primary and secondary forest at community and species level. Primary forest communities revealed typical shade tolerant traits and very low variability of traits and growth, meaning regeneration in all plots looked very similar regarding their traits. Canopy cover alone could not describe this convergence of traits, since canopy cover was similar in some some *Cecropia* and primary forest plots, however trait values varied widely between secondary forest species and within communities. Fukami et al. (2005) showed with a grassland biodiversity experiment that during succession communities converged in species traits; even so species composition remained divergent. The comparability with our study is limited, since the different forest type caused very different environments for regeneration and the succession of secondary forest will not necessarily result in a primary forest. However thinking about primary forest as an advanced successional state, our result would confirm the development of low species numbers and varying traits towards high species numbers and converged traits. The two secondary forests only differed in growth rates and herbivory, which were both strongly related to canopy cover. Canopy cover was one of the most important structural difference between secondary forests resulting from differences in land use intensity.

Appendix 4.1: Trait values (mean per species) of 26 Amazonian liana species. Sample size varies for some traits, and is indicated behind the trait. IVI is the importance index of species; main habitats are primary forest (p), *Cecropia* forest (c) and *Vismia* forest (v). RSS = ratio of stem slenderness, SLA = specific leaf area, WLR = width length ratio of the leaf and RGR = relative growth rate. Species names according to Ribeiro et al. 1999.

species	family	abbre-viation	IVI	habitat	length (cm)	RSS (cm/cm)	n	leaf size (cm²)	leaves / length (n/cm)	herbivory (%)	WLR (cm/cm)	n	SLA (m²/kg)	n	RGR (cm/(cm *yr))	n
Abuta imene	Menisperma-	Abu ime	2.29	p	24.8	110	20	35.3	0.210	6.2	0.436	20	12.06	17	-0.235	10
Abuta rufescens	Menisperma-	Abu ruf	6	p	18.9	105	66	32.5	0.240	10.5	0.493	66	20.76	50	0.138	52
Abuta sandwithiana	Menisperma-	Abu san	3.59	p	22.4	102	31	45.7	0.334	9.9	0.434	31	17.91	22	0.092	32
Adenocalymna subicanum	Bignonia-	Ade sub	3.94	c	46.0	119	47	96.7	0.236	15.1	0.295	47	15.92	45	-0.147	19
Ampelozizyphus amazonicus	Rhamna-	Amp ama	7.79	p	26.8	94	150	37.4	0.214	6.9	0.384	150	19.66	15	0.065	134
Aristolochia rumicifolia	Arsitolochia-	Ari rum	2.73	vc	57.9	528	21	31.1	0.170	5.0	0.441	21	51.63	17		
Arrabidaea egensis	Bignonia-	Arr ege	3.12	cp	59.7	102	17	65.8	0.170	19.5	0.384	17	27.10	10		
Cheiloclinium hippocrateoides	Celastra-	Che hip	2.68	p	68.1	143	20	46.0	0.735	8.3	0.323	20	13.26	18	0.074	18
Davilla sp. H	Dillenia-	Dav spH	2.47	v	19.6	76	28	58.2	0.745	5.1	0.302	28	20.44	21	0.303	25
Davilla kunthii	Dillenia-	Dav kun	2.53	v	57.4	174	25	66.5	0.421	5.6	0.433	25	18.66	23	0.399	13
Derris floribunda	Faba-	Der flo	14	p	31.6	99	286	56.1	0.165	7.1	0.490	285	21.46	68	0.060	259
Dicranostyles scandens	Convolula-	Dic sca	2.95	p	42.7	446	34	31.1	0.113	7.2	0.259	33	26.51	22	0.093	16
Doliocarpus dentatus	Dillenia-	Dol den	6.69	v	56.4	167	60	81.6	0.278	8.2	0.448	60	18.50	51	0.107	43
Machaerium ferox	Faba-	Mac fer	2.49	p	22.4	141	20	4.5	0.313	13.5	0.350	20	29.30	15		
Machaerium hoehneanum	Faba-	Mac hoe	3.44	p	34.2	127	32	27.9	0.185	7.2	0.526	32	22.07	23	0.219	16
Machaerium sp. 1	Faba-	Mac sp1	3.57	p	33.7	159	39	31.5	0.116	12.4	0.504	39	21.99	34	0.074	19
Machaerium sp. P	Faba-	Mac spP	5.97	p	20.0	132	111	17.2	0.112	5.9	0.455	111	18.42	26		
Maripa glabra	Convolula-	Mar gla	6.28	p	47.3	572	97	34.3	0.086	8.0	0.352	97	25.87	44	0.186	16
Memora adenophora	Bignonia-	Mem ade	5.39	p	45.9	106	78	26.7	0.293	12.8	0.965	78	18.45	48	0.088	71
Memora moringiifolia	Bignonia-	Mem mor	3.06	p	60.4	134	28	8.6	0.229	9.8	0.471	28	24.56	19	0.082	22
Mikania sp.	Astera-	Mikania	3.38	v	41.5	205	39	31.4	0.358	9.7	0.367	38	29.96	22	0.070	22
Odontadenia sp. A	Apocyna-	Odo spA	6.78	v	40.9	224	91	48.1	0.363	6.3	0.339	89	23.02	43	0.169	47
Paullinia sp. A	Sapinda-	Pau spA	5.55	p	12.5	96	73	10.0	0.350	10.0	0.543	73	20.36	46	0.106	52
Rourea cuspidata	Connara-	Rou cus	5.66	p	40.0	108	63	34.7	0.235	8.3	0.513	63	18.68	41	0.096	12
Senna tapajozensis	Faba-	Sentap	3.03	v	22.9	139	43	6.1	0.309	4.9	0.404	43	39.11	15	0.133	19
Smilax syphilitica	Smilaca -	Smi syp	3.11	vcp	24.9	125	24	51.0	0.226	4.6	0.357	24	19.75	19	0.292	22

5. Seed and Germination Characteristics of 20 Amazon Liana Species

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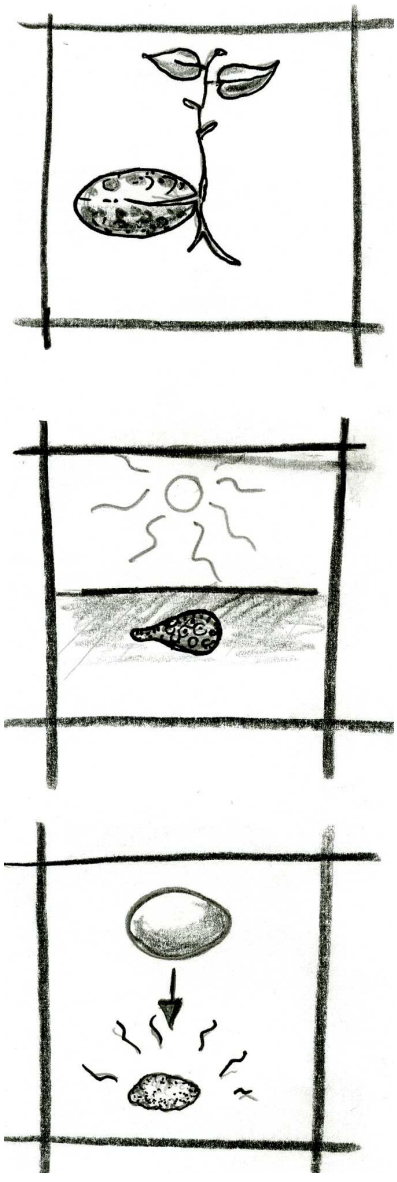


Abstract

Lianas are an important component of tropical lowland forests, influencing the dynamics of forests and may be of interest for medical purposes. For conservation, storage, cultivation and forest management, information about seed and germination characteristics of lianas could be important, but is generally scarce. For 20 Amazonian liana species we studied the seed biometry (mass, moisture content, longest and shortest axes, desiccation tolerance calculated by seed-coat-ratio) and conducted germination trials for desiccation tolerance and light dependence at constant 25 °C. For a subset of nine species germination trials at alternating temperatures (20/30 °C and 15/35 °C with 12 h light) were conducted. Dry seed mass differed 1000 fold between species (0.009 g–10.7 g), and was not correlated to fresh moisture content, which ranged from 13 to 68 %. Desiccation sensitive seeds were all above 0.27 g dry seed mass. In five species desiccation sensitive seeds were found where so far only desiccation tolerant seeds have been reported in the same genus or family. Light depending germination was found in three small seeded species (0.01 –0.015 g) and was firstly described for two, however it has to be noted that the results were based on seeds obtained once and from only one mother plant. Alternating temperature influenced germination of four out of the nine species: 15/35 °C always decreased final germination for these four species, 20/30 °C increased, decreased or did not influence germination compared to constant temperature of 25 °C. The seed and germination characteristics ranged from pioneer to climax traits, indicating that the studied species would succeed in a range of environments, such as in gaps or closed old growth forests.

Introduction

Lianas are woody climbers. They germinate on the ground, stay rooted throughout their lives and use other plants as structural support. Due to this growth form they invest few resources into structure and more in leaf and reproductive biomass (Putz & Mooney 1991). Lianas influence the dynamics of forests in various ways: they contribute to forest species diversity and offer habitat and food for canopy insects or primates (Emmons & Gentry 1983, Odegaard 2000). By connecting crowns, lianas create pathways for arboreal animals and also tear down neighboring trees in case of tree fall and are therefore a concern for forest management. They compete with trees for nutrients, water and light and can decrease tree growth and fecundity (Putz 1984, Kainer et al. 2006, Schnitzer et al. 2005) or may even increase death mortality of trees (Laurance et al. 2001). Beside edible parts, fibers or ornamental usage3, the high content of secondary compounds of many liana species is interesting for human use and may have applications as medicine or poison (Phillips 1991).

Liana seed germination is rarely studied because seeds are difficult to obtain and many species can reproduce asexually. As well as sprouting from roots, most lianas can survive when they fall down from their host trees (Putz 1984) and afterwards rapidly produce a lot of ramets by sprouting from the stem on the ground. Reproduction by seeds is however still important, as it secures genetic diversity, increases the dispersal area of a species and in case of dormant seeds could overcome adverse environmental conditions in time. Although belonging to different families, liana seeds are mainly wind dispersed and small (Gentry 1991). Particularly in naturally or anthropogenically altered areas such as tree fall gaps or secondary forests lianas occur in high densities and they are presumed to benefit from increasing areas of altered forests (Hergarty & Caballé 1991, DeWalt et al. 2000, Laurance et al. 2001, Schnitzer & Carson 2001).With the increase of secondary regrowth the importance of regeneration by seeds will change: In areas after slash and burn, succession by new dispersed seeds will be more important than in areas where the vegetation was slashed without burning where lianas can resprout from fallen stems (Roeder et al. in press). Compared to the almost stable environmental conditions in the understory of primary forest, disturbed areas are a challenge for seeds in terms of tolerance of desiccation, alternating temperature and higher irradiation.

Biometric and germination data have been intensively collected for non-cultivated seeds in temperate regions and also for many tree species in the tropics (e.g. Seed Information Database of Kew Garden, Liu et al. 2008). Yet for other growth forms of tropical forests little information exists. Useful information on seeds can be obtained from very few seeds. For example, Pritchard

et al. (2004) suggest a protocol of only 100 seeds for testing desiccation tolerance of rare species, where exploitation of seeds could be critical for the survival of the population. In our case, it was not species rareness but seed availability that restricted the number of studied seeds and species. The aim of this study on liana species of the central Amazon, Brazil, was to collect trait data connected to seeds and seed germination including desiccation tolerance, amount of seed reserves, photoblastism, temperature dependence of germination and seedling type which provide information not only for seed storage and cultivation of the species, but also for predicting success of species establishment in changing environments.

Material and Methods

Mature fruits and seeds of 20 liana species belonging to 12 families were collected close to their natural time of dispersal in the surrounding and up to 80 km north of Manaus (Table 5.1). Some of the species are subwoody to woody persistent climbers and one is a climbing shrub (*Senna* sp. 2), but were included here, referring to the liana census of Gerwing et al. (2006). It was possible to obtain seeds (used here in a broader sense for diaspore) from three to five individual plants of six species (*Anemopaegma oligoneuron, Mimosa guilandinae, Anomspermum solimoesanum, Senna* sp. 2, *Arrabidaea trailii, Passiflora nitida*); the collection of the other species was restricted to one mother plant per species. The time between collection, transport and implementation of the trials did not exceed 10 days. At arrival in the laboratory fruits and seeds were maintained at 15 °C. Immediately after extraction of the fruits, where succulent pulp was eliminated if necessary, biometric measurements were done with at least 30 seeds. For two species less seeds were available (Table 5.2). Maximal, length, width and height were measured with a digital caliper (0.01 mm). Fresh seeds were weighed individually (0.01g) and subsequently dried until constant dry mass at 105 °C for 24–62 hours (depending on seed size). Seed moisture content was calculated as the percentage of fresh mass. Seed Coat Ratio (SCR; endocarp and/or testa versus endosperm and/or embryo) was determined by dissecting 7–20 dried seeds, and the probability of desiccation tolerance or sensitivity *P* (DT/DS) was calculated based on Daws et al. (2006) in the adapted form of Gold & Hay (2008). If $P > 0.5$ seeds are probably desiccation sensitive. The ratio of shortest to longest seed axis was used to create an index for seed shape, (1 = round seed, towards 0 = flat seed).

Desiccation tolerance

Seeds were dried in two sub-samples in an air conditioned room (25 ± 4 °C, 60 ± 10 % relative humidity) above a fan until reaching equilibrium with environmental conditions, which took between five to eight days, depending on seed size. Afterwards they were dried for another seven days over the same amount of silica gel as seed mass in three layers of hermetically closed plastic bags. Seed moisture was determined for a sub-sample, as described above, and the other seeds were re-hydrated slowly for seven days in an atmosphere with saturated relative humidity, avoiding eventual imbibition damage by direct contact to water (Ellis et al. 1990), before the assessment of germination.

Germination test

Germination was assessed immediately or shortly after arrival at the laboratory. Seeds were sown on water saturated fine or medium grain vermiculite (Eucatex Agro®) in transparent plastic containers (11 x 11 x 3 cm^3 "gerbox"), or in case of small seeded species (*Senna* sp. 2, *Acacia multipinnata)* in petri dishes (9 cm diameter) with vermiculite as substrate. The containers were wrapped in loosely closed transparent, thin plastic bags to avoid excessive desiccation. Three temperature conditions were provided, each with two incubators (FANEM Mod. 347 CDG São Paulo, Brazil and LMS cooled incubator, York, UK): (i) constant temperature at 25 °C with either a 12 h photoperiod (white fluorescent light with approximately 70 µmol m^{-2} s^{-1} PAR) or in complete darkness, (ii) 12/12h alternating temperatures of 20/30 °C and (iii) 12/12h alternating temperatures of 15/35 °C, the period of higher temperature coincided with the 12 h light period in both (ii) and (iii). The thermal input for all three temperature conditions was, on average, 25 °C. For dark treatment the containers were wrapped in two layers of aluminum foil and germination was assessed only after the stabilization of the process under light conditions. Germination in light was assessed after radical protrusion (> 1 mm) and also after the development of a normal seedling (Bekendam & Grob 1979). Depending on the germination speed of the species the observations were daily, three times per week or weekly. Non germinated seeds were tested for viability at the end of the germination trials via staining (2,3,5 triphenyl tetrazolium chloride, 1 % solution) or cutting test. Seedling type was determined according to the classification of Hladik & Miquel (1990) and Garwood (1996), and described by the combination of the following traits: (P) phanerocotylar - visible cotyledons or (C) cryptocotylar - cotyledons do not emerge from seed coat, (E) epigeal - hypocotyl was elongated, or (H) hypogeal - hypocotyl was not elongated and cotyledons would remain theoretically below the soil, and (F) foliaceous cotyledons or (R)

cotyledons as reserve organs. In cryptocotylar cotyledons (C), no distinction was made if reserves were located in the endosperm or in the cotyledons.

Statistical analysis

The requirement for light during germination was determined by using the relative light germination (RLG) based on Milberg et al. (2000). The index was calculated as RLG = Gl / (Gd + Gl) where Gl = the germination percentage in light, and Gd = the germination percentage in darkness. RLG = 1 when germination is obligate light depending. The number of seeds per replicate and the number of replicates depended on seed availability (Table 5.1). Differences of germination between control and alternating temperatures were tested via Kruskal Wallis Rank Sum Test and subsequent pair wise Wilcoxon Test. Statistical analyses were carried out with R-2.8.1 (R Core Development Team 2009).

Table 5.1: List of 20 central Amazonian liana species with herbarium register at the Instituto Nacional de Pesquisas da Amazônia- INPA (Manaus, BR) and botanic family. Germination trials were conducted at 25 °C constant temperature or 12 h/12 h alternating temperatures of 20/30 °C and 15/35 °C with daily 12h photoperiod (L) or in complete darkness (D). Given are treatment per species (+) and available number of seeds and replicates. Species names according to TROPICOS (Missouri Botanical Garden 2010).

species	INPA herbarium number	family- subfamily	treatment					replicates x seed number
			fresh seed				dried seed	
			25°C L	25°C D	20/30°C L	15/35°C L	25°C L	
Acacia multipinnata Ducke		Fabaceae- Mimosoidae	+	+	n. a.	n. a	+	1 x 10
Anemopaegma floridum Mart. ex DC	231931	Bignoniaceae	+	+	+	+	+	2 x 10
Anemopaegma oligoneuron (Sprague & Sandw) Gentry	231927	Bignoniaceae	+	+	+	+	+	25 x 10
Anomospermum solimoesanum (Moldenke) Krukoff& Barneby	231935	Menispermaceae	+	+	+	+	+	5 x 4
Aristolochia silvatica Barb. Rodr.	231928	Aristolochiaceae	+	+	+	+	+	3 x 20
Arrbidaea trailii Sprague	231926	Bignoniaceae	+	+	+	+	+	4 x 16
Cissus sicyoides L.	231923	Vitaceae	+	+	+	+	+	4 x 25
Coccoloba sp.	231936	Polygonaceae	+	+	+	+	+	4 x 20
Gnetum c.f. *nodiflorum* Brongn.	231933	Gnetaceae	+	+	+	+	+	3 x 5
Matelea badilloi Morillo	231924	Apocynaceae- Asclepiadoideae	+	+	+	+	+	6 x 25
Mimosa guilandinae var. spruceana (Benth.) Barneby	231932	Fabaceae- Mimosoidae	+	+	+	+	+	5 x 20
Mucuna sp.	231940	Fabaceae- Faboideae	+	n. a	n. a	n. a	+	2 x 3
Passiflora c.f. *acuminata* DC.		Passifloraceae	+	+	n. a	n. a	+	2 x 15
Passiflora nitida HBK	231937	Passifloraceae	+	+	+	+	+	8 x 25
Paullinia c.f. *capreolata* (Aubl) Radlk.	231939	Sapindaceae	+	+	+	+	+	2 x 20
Paullinia rugosa Benth. ex Radlk.	231938	Sapindaceae	+	+	n. a	n. a	+	2 x 10
Senna sp. 2	231922	Fabaceae- Caesalpinioideae	+	+	+	+	+	9 x 12
Smilax sp.	231930	Smilaceae	+	+	n. a	n. a	+	1 x 10
Strychnos c.f. *amazonica* Krukoff	231925	Loganiaceae	+	+	n. a	n. a	+	1 x 10
Strychnos glabra Sagot ex Progel	231929	Loganiaceae	+	+	+	+	+	2 x 10

Results

Seed biometrics and seedling characteristics

The range of seed sizes covered three orders of magnitude from 0.0085 g (*Matelea badilloi*) to 10.7 g dry seed mass *(Mucuna* sp.). The length of the longest seed axes differed eight fold in the extremes, from 5.1 mm (*Coccoloba* sp.) to 38.8 mm (*Mucuna* sp., Table 5.2, Appendix 5.1). Large seeds were rounder than smaller ones, and seed shape index correlated positively with seed dry mass (Pearson's R = 0.609, *P* = 0.004, data of seed mass was log transformed). Seed moisture content at dispersal for all species ranged between 13–70 % and was not significantly correlated to dry seed mass (Pearson's R = 0.385 *P* = 0.094, data of seed mass log transformed, Fig. 5.1).

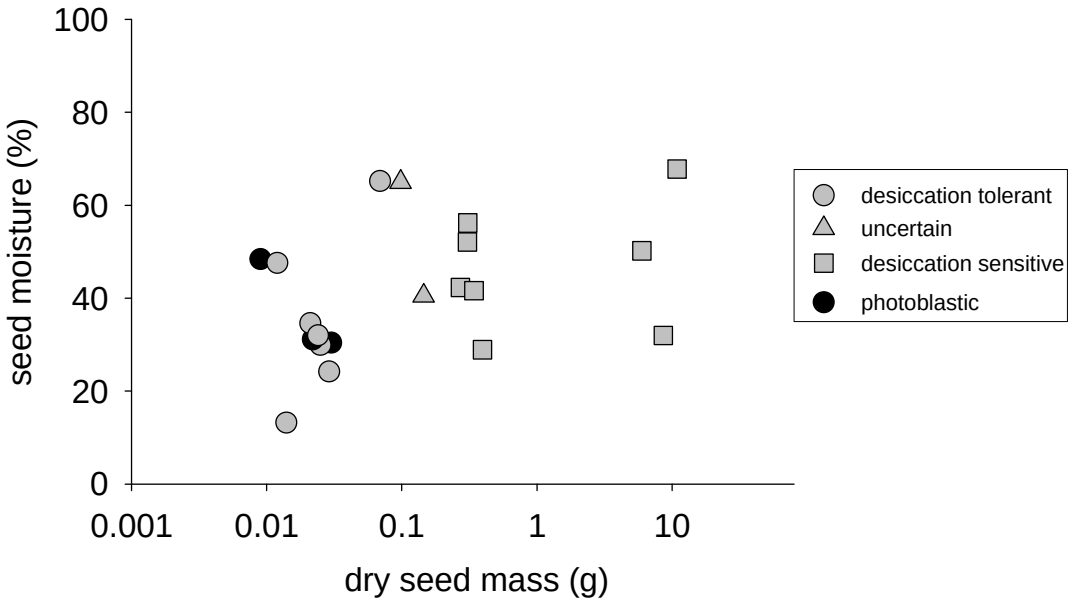


Fig 5.1: Seed moisture at dispersal of 20 liana species of the central Amazon in relation to seed size (dry mass) with indication of desiccation tolerance or desiccation sensitivity of the seeds and necessity of light for germination (photoblastic seeds). Note log-scale at x-axis.

The seedling type of nine small seeded species (dry seeds mass < 0.03 g) was phanerocotylar epigeal with foliaceous or reserves holding cotyledons (PEF or PER, Table 5.2). Above 0.07 g dry seed mass the seedling type was cryptocotylar hypogeal (CHR) with the exception of two species with PEF seedling type (*Coccoloba* sp. 0.15 g and *Strychnos amazonica* 0.31 g).

Desiccation tolerance

Species were clearly separated into desiccation tolerant and desiccation sensitive seeds along the dry seed mass axis (Fig. 5.1). The ten smaller seeded species (up to 0.07 g dry seed mass) germinated after desiccation to a moisture content < 9% (3.7–8.8%) and had a calculated probability of desiccation tolerance P (DT/DS) < 0.5 (Table 5.2). Eight species with dry seed mass > 0.27 g (*Paullinia rugosa, Paullinia capreolata, Strychnos amazonica, Strychnos glabra, Smilax* sp., *Gnetum nodiflorum*, *Anomospermum solimoesanum, Mucuna* sp.) did not germinate after desiccation, and probability calculation was in accordance (*P* (DT/DS) > 0.5). The large seeds of *Gnetum nodiflorum* and *Anomospermum solimoesanum*, though dried for 15–20 days, still contained 17% and 12% moisture content respectively at the implementation of germination trails after desiccation. Two species (*Coccoloba* sp. and *Anemopaegma floridum*) did not germinate after desiccation (0% germination) but should be desiccation tolerant according to the calculated probability *P* (DT/DS) = 0.22 and 0.06 respectively.

Light germination

Two species (*Matelea badilloi* 0.009 g, *Aristolochia silvatica* 0.03 g) needed light for germination (photoblastic seeds), RLG was ≥ 0.99 , as there was no germination in darkness and germination in light was 60% and 90% respectively. *Cissus sicyoides* (0.02 g), with 25% germination in darkness and 93% in light, had a RLG of 0.79. Three more species had RLG ≥ 0.68 (Tab. 5.2), but repetition size (*Anemopaegma floridum, Passiflora acuminata*, Table 5.1) or germination of the control was very low (*Gnetum nodiflorum*, one seed). Thus data interpretation should be done cautiously.

Table 5.2: Seed and germination characteristics of 20 liana species ranged by increasing dry seed mass. Given are mean ± standard deviation and sample size (n), dessication tolerance (DT) and dessication sensitivity (DS) based on germination trials (G) and probability (*P*) of desiccation sensitivity calculated after Daws et al. (2006), relative light germination (RLG) determined after Milberg et al.(2000), time for germination of 1st seed and of 50 % of germinable seeds and seedling type P= phanerocotylar , C=cryptocotylar , E= epigeal, H= hypogeal, F= foliaceous cotyledons or R= reserve cotyledons. In case of winged seeds, fresh seed mass and longest axis included wings.

species	fresh seed mass (g)	n	seed moisture (%)	n	longest axis (mm)	n	seed shape	*P* (DT/DS)	G (DT/DS)	RLG	germination time (d)		seedling type
											1st	50%	
M. badilloi	0.016 ± 0.002	50	48.4 ± 2.9	50	8.9 ± 0.4	50	flat	0.001	DT	0.99	5	15	PEF
P. acuminata	0.021 ± 0.005	15	47.6 ± 11.6	14	7.3 ±0.3	30	flat	0.017	DT	0.68	92	105	PEF
M. guilandinae	0.016 ± 0.005	30	13.2 ± 5.2	30	7.0 ± 0.9	60	flat	0.055	DT	0.58	5	9	PEF
Senna sp. 2	0.031 ± 0.008	50	34.6 ± 3.3	50	6.4 ± 1.0	50	oval	0.002	DT	0.52	2	2.5	PEF
C. sicyoides	0.031 ± 0.002	30	31.1 ± 3.2	30	5.1 ± 0.3	30	drop like	0.010	DT	0.79	11	24	PEF
P. nitida	0.033 ± 0.006	50	32.0 ± 3.4	50	7.0 ± 0.7	50	flat	0.001	DT	0.58	108	156	PEF
A. trailii	0.035 ± 0.008	41	29.9 ± 8.8	41	29.2 ± 4.4	41	winged & flat	0.037	DT	0.51	11	23	PER
A. multipinnata	0.037 ± 0.008	30	24.2 ± 3.5	14	6.4 ± 0.7	30	flat	0.068	DT	0.53	3	3	PER
A. silvatica	0.035 ± 0.004	30	30.4 ± 3.2	30	18.6 ± 1.9	30	winged & flat	0.022	DT	1.00	10	84	PEF
A. oligoneuron	0.191 ± 0.042	60	65.2 ± 3.6	60	38.7 ± 4.3	60	winged & flat	0.026	DT	0.57	14	16	CHR
A .floridum	0.396 ± 0.037	30	65.0 ± 3.7	10	52.9 ± 4.8	30	winged & flat	0.060	DS	0.71	21	31	CHR
Coccoloba sp.	0.238 ± 0.051	51	40.5 ± 3.8	51	7.7 ± 0.6	51	round	0.222	DS	0.53	31	70	PEF
P. rugosa	0.464 ± 0.097	30	42.3 ± 3.9	10	10.0 ± 0.8	30	round	0.780	DS	0.51	9	12	CHR
S. amazonica	0.691 ± 0.221	30	52.1 ± 3.1	11	14.9 ± 1.8	30	triangular	0.523	DS	0.51	22 n=6	36 n=6	PEF
S. glabra	0.776 ± 0.101	30	56.2 ± 3.1	10	12.4 ± 0.7	30	triangular	0.814	DS	0.42	20	26	CER?
Smilax sp.	0.584 ± 0.123	30	41.6 ± 3.1	10	11.3 ± 1.2	30	triangular	0.770	DS	0.42	20	29	CHR
P. capreolata	0.477 ± 0.051	10	28.9 ± 3.1	10	13.3 ± 0.5	30	oval	0.814	DS	0.50	4	6	CHR
G. nodiflorum	12.19 ± 2.346	46	50.2 ± 3.4	19	43.2 ± 3.1	46	oval	0.977	DS	1.00 n=1	155 n=1	155 n=1	CHR
A. solimoesanum	13.97 ± 2.603	84	32.0 ± 3.2	22	36.1 ± 2.6	84	oval	0.543	DS	0.63	91	157	CHR
Mucuna sp.	34.16 ± 12.002	25	67.8 ± 3.2	9	38.8 ± 5.7	25	round	0.984	DS	na	53 n=4	53 n=4	CHR

Germination at constant and alternating temperatures

Final germination of the seeds at constant 25 °C with light was above 90% for eight species (*Anemopaegma floridum, A. oligoneuron, Aristolochia silvatica, Arrabidaea trailii, Cissus sicyoides, Paullinia capreolata, P. rugosa, Senna* sp. 2), between 61–88% for five species (*Acacia multipinnata, Anomospermum solimeosanum, Matelea badilloi, Mucuna* sp. *Strychnos glabra*), and 32–50% for four species (*Coccoloba* sp. *Passiflora acuminata, Smilax* sp. *Strychnos amazonica*). The lowest final germination were found at *Passiflora nitida* (20%) and *Gnetum nodiflorum* (7%). Seed viability of all seeds at the end of the germination trials (excluding the desiccation treatment) was > 91% for ten species, four species had between 78–88% (*Matelea badilloi, Mimosa guilandinae*, *Coccoloba* sp., *Strychnos glabra*), *Mucuna* sp. had 67% and *Strychnos amazonica* had 55% seed viability; three species were not tested (*Passiflora acuminata, Passiflora nitida, Gnetum nodiflorum*).

Amongst all species, the time required until the first seed showed radicle protrusion at the constant temperature of 25 °C was between two to 155 days. In six species (two Fabaceaes, two Sapindaceaes and an Apocynaceae) first germination occurred after two to nine days and 50% germination of germinable seeds was reached within 15 days (Table 5.2). Four species (*Passiflora acuminata, Passiflora nitida, Gnetum nodiflorum, Anomospermum solimeosanum)* needed more than 90 days for the protrusion of the radical (Table 5.2).

Germination at alternating temperature was tested with 15 species. For six species repetition size was too low for further statistical analysis (*Acacia multipinnata, Anemopaegma floridum, Anomospermum solimeosanum, Gnetum nodiflorum, Paullinia capreolata, Strychnos glabra,* Table 5.1) and germination success at alternating temperatures did not deviate more than 10% from germination at constant 25 °C. Exceptions were *Strychnos glabra* with 40% less germination at 15/35 °C and *Anomospermum solimoesanum* with 36% less germination at 20/30 °C. *Gnetum nodiflorum* had two germinated seeds at 20/30 °C and none at 15/35 °C.

For nine species a comparison between germination at constant and alternating temperature could be analysed statistically (Table 5.3). Five species (*Arrabidaea trailli, Anemopaegma oligoneuron, Cissus sicyoides, Mimosa guilandinae, Senna* sp. 2) had similar final germination at alternating and constant temperatures, and final germination was ≥ 90% at all temperature conditions, except for *Mimosa guilandinae*. For these species germination was slightly delayed (*Senna* sp. 2, *Anemopaegma oligneuron*) or accelerated (*Cissus sicyoides, Arrabidaea trailii*) by alternating temperatures at 15/35 °C (Fig 5.2). Alternating temperatures

affected final germination in four species: *Aristolochia silvatica* and *Coccoloba* sp. reached the same final germination result with constant temperature or with a small daily temperature cycle (30/20 °C), however with the larger daily temperature cycles (35/15 °C) germination dropped down to 0% and 5% respectively. Repetitions for *Aristolochia silvatica* were insufficient for Kruskal-Wallis–Rank Sum test (Table 5.3), but an ANOVA revealed significant differences ($F = 66.6$, $df = 23$, $P < 0.001$, Tukey post hoc test constant 25 °C versus 15/35 °C, $P > 0.001$). *Matelea badilloi* had the highest germination with small daily temperature cycles (20/30 °C, 84%), intermediate at constant temperature (52%) and no germination with a large temperature cycling (35/15 °C). *Passiflora nitida* only germinated at constant 25 °C (Table 5.3, Fig. 5.2).

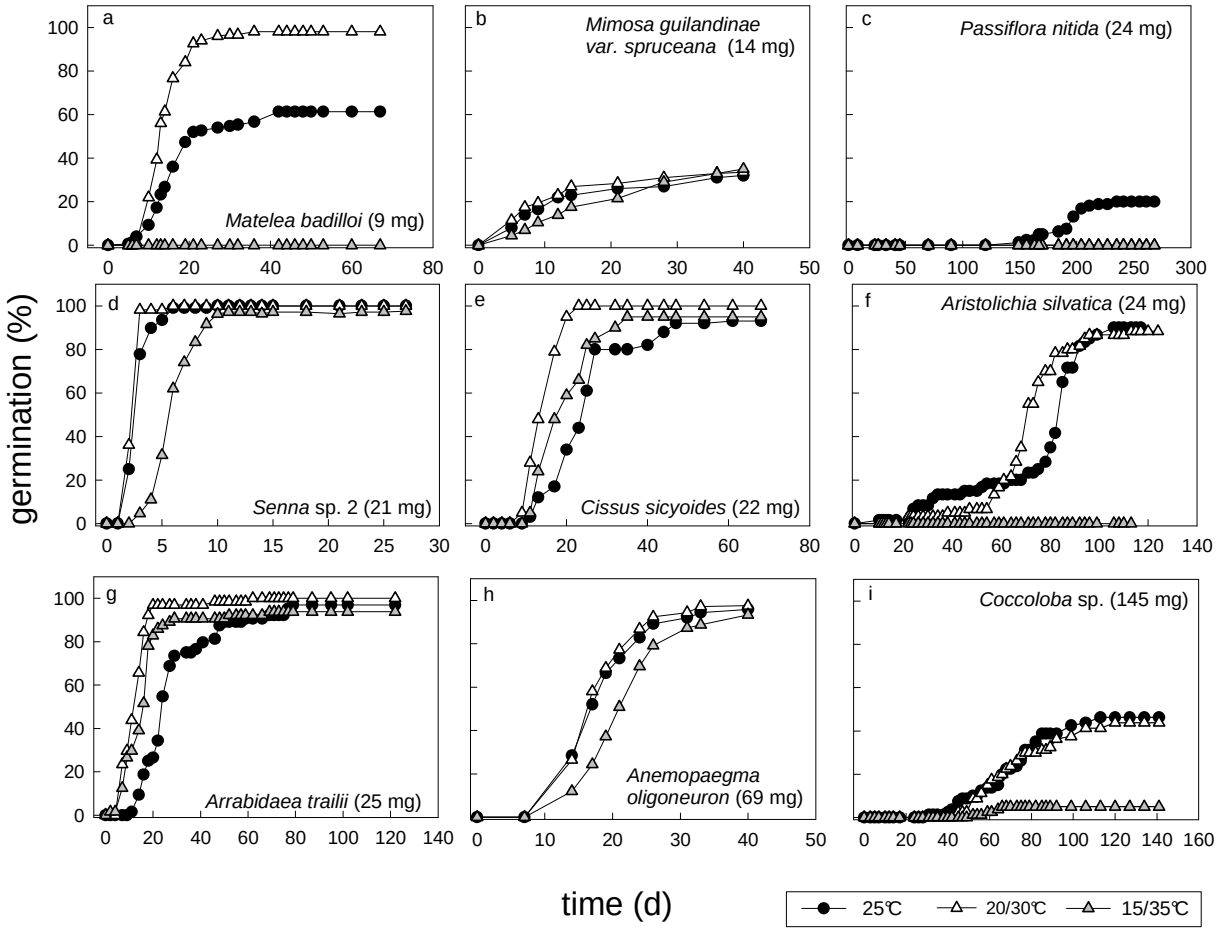


Fig. 5.2: Germination curves of nine liana species (a-i) of the central Amazon at constant (25 °C) or 12/12h alternating temperatures (20/30 °C, 15/35 °C) with 12 h light daily. The species were ranged by increasing dry mass of embryo and endosperm (dry mass of whole seed is given in brackets). For significant differences between temperature conditions see Table 5.3.

Table 5.3: Germination percentage (mean ± SD) of nine liana species, ranged by increasing embryo and endosperm dry mass, at three temperature conditions: constant temperature of 25°C and 12/12h alternating temperatures of 20/30°C and 15/35°C. Results of Kruskal-Wallis-Rank Sum-Test (Chi-square-value, degrees of freedom) for differences over all treatments and results of subsequent pair-wise Wilcoxon-test. Significance levels * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.
(***) result of ANOVA, as replicate number was not sufficient (see Table 5.1)

species	X^2	25°C	20/30°C	15/35°C
Matelea badilloi	**15.70*** **	**2 ± 10a**	**84 ± 7b**	**0 ± 0c**
Mimosa guilandinae var. spruc.	0.31	2 ± 15a	33 ± 10a	35 ± 7a
Passiflora nitida	**14.93*** **	**20 ± 22a**	**0 ± 0b**	**0 ± 0b**
Senna sp. 2	4.16	100 ± 0a	100 ± 0a	98 ± 4a
Cissus sicyoides	5.49	3 ± 2a	100 ± 0a	95 ± 6a
Aristolichia silvatica	**5.64(***)**	**90 ± 10a**	**88 ± 16a**	**0 ± 0b**
Arrabidaea trailii	2.64	95 ± 6a	100 ± 0a	94 ± 9a
Anemopaegma oligoneuron	3.49	96 ± 7a	97 ± 5a	92 ± 10a
Coccoloba sp.	**7.50***	**46 ± 13a**	**44 ± 20a**	**5 ± 4b**

Discussion

The 20 tested species represented perhaps 5–7% of local liana species. In a reserve (100 km^2) close to Manaus, around 300 liana species were found (Ribeiro et al. 1999). Five species (*Mimosa guilandinae, Senna* sp. 2, *Passiflora nitida, Arrabidaea trialii, Acacia multipinnata*) are very frequent and found mainly in disturbed areas or secondary regrowth, four other species (*Matelea badilloi, Aristolochia silvatica, Anemopaegma floridum, Anomospermum solimoesanum*) are considered as rare and mainly occur in primary forest (Ribeiro et al. 1999). The remaining species, where information was available, had intermediate frequencies and their habitats varied form forest valley bottoms to disturbed areas. A wide variety of morphological traits and physiological responses to environmental factors was found, e. g. the very large seeds of *Mucuna* species. The time required for germination exhibited a whole gradient from fast (less than a week) to slow germinating (several months) species and no common trait in germination velocity could be found. Two species which needed more than three months for germination belonged to the Passiflora-family (*Passiflora acuminata, Passiflora nitida*), which is known for its seeds with physiological dormancy (e.g. Passos et al. 2004).

Seedling types could be separated by seed size: the smaller seeded species (≤ 0.02 g dry seed mass) had seedlings with elongated hypocotyls and foliaceous, photosynthetic active

cotyledons (PEF), in species with dry seed masses from 0.07–0.3 g several seedling types occurred, above 0.34 g dry seed mass only CHR seedling types were found. Even within one family (Bignoniaceae) seedling types varied for species with different seed masses: *A. trailii* (dry seed mass 0.025 g) had visible cotyledons, where as the cotyledons of two larger seeded species (*Anemopaegma oligoneuron* 0.07 g and *Anemopaegma floridum* 0.1 g) stayed in the seed coat (cryptocotylar) (Table 5.2). In agreement to our findings, other extensive studies have found that the proportion of species with cryptocotylar, hypogeal seedling type continuously increased, and the occurrence of PEF type decreased with seed size (e.g. Wright et al. 2000, 1744 species, all life forms; Ng 1978, 209 tropical tree species). For a seed size of 0.3–2.0 cm, which is similar to the seed size of most of the species presented here, 65–79% of all tree species had epigeal seedlings in an Asian tropical forest (Ng 1978), and ~25–30% of liana species had PEF seedling type in African rain forest (Hladik & Miquel 1990). The continuum of seedlings types along the seed size axis might explain the occurrence of two species of PEF seedling type with rather large seeds in the scale of our study (*Coccoloba* sp. with 0.15 g and *Strychnos amazonica* with 0.31 g dry seed mass). Families of both species (Polygonaceae and Loganiaceae) are known to have phanerocotylar seedlings (Watson & Dallwitz 1992, Zanne et al. 2005). PEF and CHR were found to be the dominating seedling types in tropical forests (Ibarra-Manríquez et al. 2001), and in a ecological view, they should select for different environments: Species with larger seeds and CHR seedling type should be shade tolerant and typically be found inside the forest (Foster 1986, Hladik & Miquel 1990), however of the liana species with CHR seedling type presented here, some occurred in old growth forest and others in disturbed areas. Seedling type PEF is the most successful establishment strategy in high light environments (Hladik & Miquel 1990), which concords with the fact that all of our studied species of altered areas had this seedling type. *Matelea badilloi* and *Aristolochia silavtica*, which are both recorded as rare old growth forest species also had foliaceous epigeal seedlings, suggesting that germination of these species depends on forest gaps. Although lianas are generally considered as light loving growth forms, which would select for mainly PEF seedling type, so far no different pattern of seedling type frequency between trees and lianas could be found in forest communities of Mexico and Gabon (Hladik & Miquel 1990, Ibarra-Manríquez et al. 2001) and in the present study as well not a single seedling type dominated.

Desiccation tolerance

Desiccation tolerance was estimated by the calculation of desiccation tolerance probability based on seed coat ratio (Daws et al. 2006, Gold & Hay 2008) and from results of the germination test (see Table 5.2). All ten species that were desiccation tolerant in our survey belong to families or genera with seeds known to be desiccation tolerant, for *Cissus sicyoides* species records even exist (Liu et al. 2008). Some *Passiflora* species, e.g. *P. edulis* are known to have seeds with intermediate storage behaviour (Black et al. 2006), meaning that they tolerate desiccation until around 8% moisture content (Ellis et al. 1990) but not below 5% like so called orthodox seeds (Roberts 1972). In our study design it could not be revealed if *P. acuminata* and *P. nitida* had intermediate seeds as well.

Desiccation sensitive seeds were found in eight species. A well studied species of economic importance in the Amazon region, *Paullinia cupana* (Sapindaceae) is recorded to have desiccation sensitive seeds (Lleras 1994) which supports our finding in the same genus for *P. rugosa* and *P. capreolata*. For the genera *Smilax, Strychnos, Gnetum* and *Mucuna* so far no records of desiccation sensitive seeds were found, congeners had been mentioned to be desiccation tolerant (Liu et al. 2008). No seed information was found for the genus *Anomospermum,* the few investigated species of the same family (*Menispermaceae*) all had desiccation tolerant seeds (Liu et al. 2008). The mentioned records often included smaller seeded species and partly from temperate regions. Desiccation sensitive seeds are most common in the tropics, and therefore the probability to find a species with desiccation sensitive seeds of a certain genus or family is higher in tropical than in temperate regions (Pammenter & Berjak 2000). Also the percentage of species with desiccation sensitive seeds increases with increasing seed size (Hong & Ellis 1996). For the presented species, all seeds above 0.27 g dry mass were desiccation sensitive. Another parallel increase connected to desiccation sensitivity is that of seed size and moisture content, the positive relationship of the two traits was proved in former studies (e.g. Hong & Ellis 1998). However no such correlation was found in the twenty species tested in this study (Fig 5.1). As seeds were weighed immediately after collection or separation of the fruits, fresh weight and moisture content of the winged or hair tuft (coma) bearing species (*Matelea badilloi, Arrabidaea trailii, Anemopaegma oligoneuron, A. floridum and Aristolochia silvatica*) may be slightly overestimated, as these seeds would probably dry for a few hours or days in the opened fruit before being dispersed by wind. Hong and Ellis (1996) also stated that for seeds of 25–55% moisture content at shedding and for a wide range of seed sizes, no prediction about desiccation tolerance can be drawn from these two traits (size and moisture content). Desiccation

sensitive seeds are expected to shed during the rainy season to avoid any risk of severe water loss. In our study, seeds of five desiccation sensitive species were shed at the end or beginning of the rainy season (June, July and Nov.) and three shed during the rainy season (April, May). Desiccation tolerant seeds were shed during both the rainy and dry season.

Two species revealed contradicting results in the germination test and calculated probability of desiccation tolerance (*Coccoloba* sp., Polygonaceae and *Anemopaegma floridum*, Bignoniaceae). Regarding the phylogenetic relationship both species could have desiccation tolerant seeds, as in the Bignoniaceae family only species with desiccation tolerant seeds are known (Liu et al. 2008), and for Polygonaceae so far only one tree with desiccation sensitive seeds (*Triplaris cumingiana*) has been recorded (Anno. 1993, Liu et al. 2008). The lack of germination after drying might be caused by unripe seeds, which have not acquired the desiccation tolerance at the end of maturation drying (e.g. Hong & Ellis 1997). However *Coccoloba* sp. seeds were harvested several times within two weeks from the same mother plant. In doubtful cases, the calculation of *P* (DT/DS) was more reliable, because biometric data were more robust against difficulty in knowing exactly the right time of harvest than germination tests.

Light germination

The high RLG of *Aristolochia silvatica*, *Matelea badilloi* and *Cissus sicyoides* suggest that these seeds could be considered as photoblastic. Repetition size was sufficient (at least 3 x 20 seeds), yet results are not totally reliable because seeds were harvested only from one matrix. To our knowledge this is the first record indicating photoblastism of *Aristolochia silvatica* and *Matelea badilloi*. Photoblastism of *Cissus sicyoides* has already been documented in a field study (Sanches & Válio 2002). The three listed photoblastic species all had small seeds (0.009–0.03 g dry mass). For small seeds with restricted resources light is required soon after germination to support growth for photosynthetic self sufficiency. Thus with increasing seed size, light dependence of seed germination is reduced as shown for different growth forms (herbaceous plants, trees) in tropical and temperate zones (Milberg et al. 2000, Jankowska-Blaszczuk & Daws 2007, Pearson et al. 2002). Besides the above mentioned cases the whole range of RLG values between 0.71 and 0.42 was found, however low repetition size (*Anemopaegma floridum*, *Passiflora acuminata*, *Smilax* sp., *Strychnos amazonica*) or low germination of the control (*Gnetum nodiflorum*, RLG = 1, one seed germinated) does not allow an indication of light influence on germination at the current time.

Alternating temperature

The understory of old growth tropical forest presents a habitat of low temperature fluctuations compared to open areas such as gaps (Pearson et al. 2002), borders or secondary forests. In this study the different environments were represented by constant temperature and two regimes of alternating temperatures. Oscillation of temperature induced two responses: The final germination was close to that of constant temperature, or seeds did not germinate at all or at very low rates. However, in some species only the high temperature fluctuations reduced germination. Only one species (*Matelea badilloi*) benefitted from low oscillations (20/30 °C). In former studies the influence of alternating temperature on germination was connected to seed size: Small seeded tropical pioneer species (0.04–0.68 mg) were found to be intolerant to temperature fluctuations whereas for relatively larger seeds (> 2 mg) germination rate increased (Pearson et al. 2002). Taking an ecological view, this intolerance may prevent small seeded species germinating in unfavorable conditions for seedling establishment e.g. high irradiation and drought in large clearings, though these species still depend on smaller vegetation gaps for seedling establishment. For larger seeds the impact of alternating temperatures should be less inhibiting, since high resources made the germination process more independent of environmental parameters, or could even act as a signal of the presence of large gaps and encourage germination (Pearson et al. 2002) For the species presented in this study no specific pattern of germination response to temperature fluctuations was found with increasing seed resources (embryo and endosperm dry mass). However the size scale for the nine tested species was somewhat limited, ranging from 3–124 mg embryo dry mass, extremely small seeded species were missing.

As summarized by Probert (2000) temperature cycles were found to stimulate germination for many species and was often linked to photoblastism. Alternating temperatures may enhance stimulation through light or even enable dark germination of initially photoblastic seeds. However, in the present study one species with photoblastic seeds (*Cissus sicyoides*) tolerated alternating temperatures and the two others did not (*Matelea badilloi, Aristolochia silvatica*); the combination of dark germination and alternating temperatures was not tested here. This indicates that species of the same growth form with photoblastic seeds still differ in their niche of regeneration.

One pattern observed in our study was related to the velocity of germination. Fast germinating species (first germination between 2–14 days, 50% of germinable seeds germinated between 2.5–24 days) were indifferent to alternating temperatures (one exception: *Matelea*

badilloi). This germination behavior suggests that thermal settings in open areas as well as in closed forests suits these species to germinate. For slow germinating or dormant seeds, high temperature fluctuations inhibited germination. For example the dormancy of *Passiflora nitida*, which is at least partially physiological (Passos et al. 2004) could not broken by alternating temperatures but was probably even enhanced.

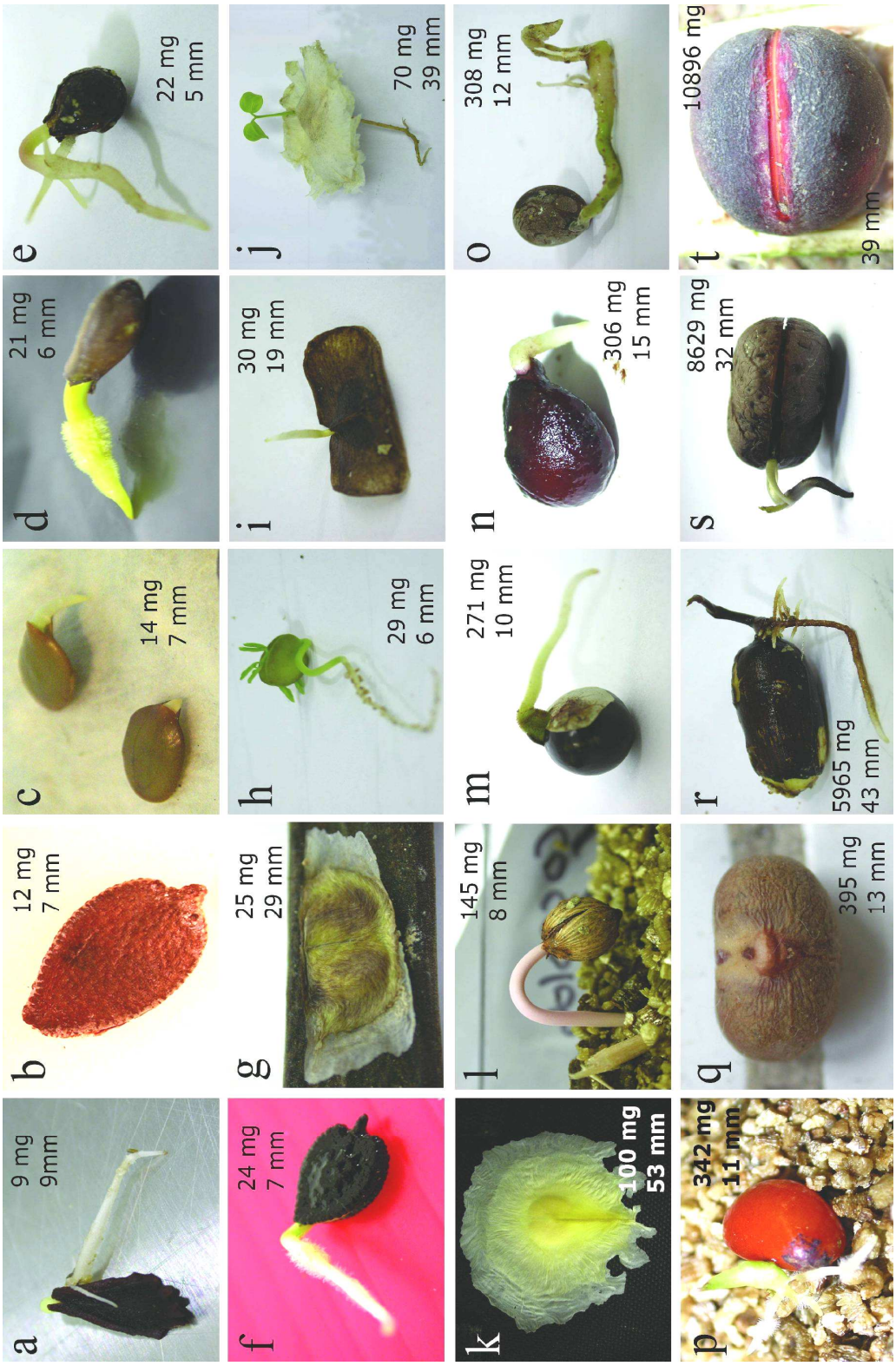
Conclusion

The present study covers perhaps 5% of Amazonian liana species and cannot describe seed and germination traits of the whole liana community in the area. Nevertheless, serving as a pilot study much information can be drawn:

Desiccation sensitivity of seeds was not known for five out of 20 liana species, light depending germination was firstly described for *Aristolochia silvatica* and *Matelea badilloi*. However it has to be noted that the results were based on seeds obtained once and from only one mother plant, and we could not validate our results on larger sample sizes.

The growth form of liana is very diverse; this evidence applies also to seed, seedling and germination characteristics. We could identify typical pioneer species (photoblastic, desiccation tolerant seeds and PEF seedling type), climax species (large, desiccation sensitive seeds with CHR seedling type) and species with trait combinations in between. The survey of morphological and physiological traits provided redundancy of results in cases of low germination success. Regarding the adaptation to disturbed habitats, simplified here by alternating temperatures, we found contrasting responses in a small range of seed size (9–145 mg). It implicates that establishment of lianas from seeds is restricted to very species specific niches.

It would be very supporting for any future use of lianas (cultivation, conservation and research) to continue a screening including morphological and physiological seed data from any available sample size to obtain minimum information for storage and germination behaviour.



Appendix 5.1: Images of fresh or germinating seeds of all studied liana species. Given are the average dry seed mass and the average longest axis of fresh seed (including wings). a) *Matelea badilloi*, b) *Passiflora acuminata*, c) *Mimosa guilandinae var. spruceana*, d) *Senna* sp. 2, e) *Cissus sicyoides*, f) *Passiflora nitida* g) *Arrabidaea trailii*, h) *Acacia multipinnata*, i) *Aristolochia silvatica*, j) *Anemopaegma oligoneuron*, k) *Anemopaegma floridum*, l) *Coccoloba* sp., m) *Paullinia rugosa*, n) *Strychnos amazonica*, o) *Strychnos glabra*, p) *Smilax* sp. q) *Paullinia capreolata*, r) *Gnetum nodiflorum*, s) *Anomospermum solimoesanum*, t) *Mucuna* sp..

6. Conclusions

Even though lianas are recognized as an influential component of tropical forests, and studies of lianas have exploded in the last few years, information about liana regeneration remains scarce. This dissertation combines aspects of seed and germination biology with natural regeneration in different forest communities. Despite low rates of liana species coverage due to logistic constraints, this is pioneering work for the Central Amazon, and some overall conclusions can be drawn:

The growth form liana comprises a broad range of leaf, plant and seed traits emphasising the functional diversity of the group. Remarkable differences of regeneration modes between liana species were found in seed characteristics, germination behavior and in the traits and growth of seedlings, saplings and sprouts in over all sites. The found strategies ranged from typical features of successional and pioneer species to climax species, indicating that liana species may succeed in a range of environments.

The well known high abundance of lianas in disturbed areas could be confirmed for mature plants in the presented work, but only in forests without intensive land use before succession. Stem densitity of mature lianas was decreased in areas that suffered more intense disturbance (burning and grazing) before forest succession. The influence of land use history on liana regeneration was less obvious, but was found in small details such as the high percentage of fibrous lianas. Repeated burnings and land use as pasture before forest succession led to low diversity in liana regeneration, a finding that confirms observations in trees (e.g. Mesquita et al. 2001).

During succession the environmental conditions for regeneration change continuously and predictions of future vegetation are difficult, because many stochastic and deterministic factors are included in this process (Chazdon 2008). The success of liana regeneration during succession will depend on the intensity and kind of disturbance, the presence of seed sources or vegetative organs and crucially on species identity.

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Hiermit versichere ich, dass ich die alleinige Autorin der vorliegenden Doktorarbeit bin und diese nur mit den angegebenen Quellen und Hilfsmitteln angefertigt habe. Alle Stellen, die aus den Quellen entnommen wurden, sind als solche gekennzeichnet. Diese Arbeit wurde bisher nicht in gleicher oder ähnlicher Form in einem anderen Promotionsverfahren vorgelegt.

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